Evaluation of eutrophication and water level drawdown on Lake Whitefish (*Coregonus clupeaformis*) productivity; Fish habitat assessment

Sonya Havens, Michael Rennie, Paul Blanchfield, Michael Paterson and Scott Higgins

Fisheries and Oceans Canada
Freshwater Institute
Science Branch
501 University Crescent
Winnipeg, Manitoba
R3T 2N6

2014

Canadian Technical Report of
Fisheries and Aquatic Sciences No. 3110

Fisheries and Oceans Canada Pêches et Océans Canada

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base Aquatic Sciences and Fisheries Abstracts.

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457-714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715-924 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destines essentiellement à un public international et ils sont distribués à cet échelon. II n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la base de données Résumés des sciences aquatiques et halieutiques

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 456 de cette série ont été publiés à titre de Rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de Rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de Rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Canadian Technical Report of
Fisheries and Aquatic Sciences No. 3110

2014

Evaluation of eutrophication and water level drawdown on Lake Whitefish (*Coregonus clupeaformis*) productivity; Fish habitat assessment

Sonya Havens, Michael Rennie, Paul Blanchfield, Michael Paterson and Scott Higgins

Fisheries and Oceans Canada
Freshwater Institute
Science Branch
501 University Crescent
Winnipeg, Manitoba
R3T 2N6

Cat. No. Fs 97-6/3110E-PDF ISBN 978-1-100-25287-2

Correct citation for this publication:

Havens, S., Rennie, M., Blanchfield, P., Paterson, M. and Higgins, S. 2014. Evaluation of eutrophication and water level drawdown on Lake Whitefish (*Coregonus clupeaformis*) productivity; Fish habitat assessment. Can. Tech. Rep. Fish. Aquat. Sci. 3110: vi + 40 p.

ABSTRACT

Havens, S., Rennie, M., Blanchfield, P., Paterson, M. and Higgins, S. 2014. Evaluation of eutrophication and water level drawdown on Lake Whitefish (*Coregonus clupeaformis*) productivity; Fish habitat assessment. Can. Tech. Rep. Fish. Aquat. Sci. 3110: vi + 40 p.

Large-scale habitat disruptions can affect the productivity of fish species important to commercial, recreational and aboriginal fisheries. In many cases changes in fish productivity may not be detected due to the difficulty obtaining sufficiently robust estimates of population abundance or age class strength through time. In the absence of direct and robust measures of fish productivity there is a need for the development and assessment of physical, chemical and biological indicators that link fish productivity to habitat disruptions. Such indicators may be useful for regulatory decision making for approvals for habitat disruptions, and offsets for potential losses to fish productivity.

The goal of this study was to evaluate the effect of eutrophication and winter water-level drawdown on the habitat of Lake Whitefish. The experimental eutrophication of the northeast basin (NEB) of Lake 226 (L226) at the Experimental Lakes Area between 1973-80 resulted in the reduction, and in some years, elimination, of optimal Lake Whitefish habitat as defined by physiological requirements for temperature (≤ 12 °C) and dissolved oxygen (≥ 4 mg/L). These changes primarily resulted from the effects of eutrophication on the volume of well oxygenated water within the hypolimnion and metalimnion, rather than potential changes to the depth of the 12 °C isopleth, which remained relatively stable. The volume of water where thermal and dissolved oxygen (DO) conditions were optimal for Lake Whitefish (i.e. physiological habitat) declined more rapidly after thermal stratification was reached within the eutrophication experiment than the control. Therefore, the number of days where habitat was moderately (<10% of habitat available) or severely (<1% of habitat available) restricted increased by ~60 days, and ~30 days, respectively. The effect of experimental lake-drawdown during winter months influenced Lake Whitefish habitat by reducing the volume of water that met both thermal and O_2 optimal requirements. While lake-draw down did not influence the production or transfer of organic matter, or rates of sediment O_2 demand, reductions in hypolimnetic volume reduced the total potential habitat available and increased the O_2 depletion rate. Overall, the number of days where habitat was moderately or severely restricted increased by 44 days, and 2 days respectively. Because Lake Whitefish diets are primarily reliant on benthos, reductions in optimal physiological habitat (i.e. lake volume) also led to concurrent reductions in optimal foraging habitat (area of lake-bottom where thermal and DO are optimal). Presumably, the reduction in optimal foraging habitat would result in increased competition for resources, increased feeding forays outside of optimal conditions, or a combination of both responses and lead to a reduction in Lake Whitefish condition, abundance, and productivity.

Havens, S., Rennie, M., Blanchfield, P., Paterson, M. and Higgins, S. 2014. Évaluation de l'eutrophisation et de l'abaissement du niveau d'eau sur la productivité du grand corégone (*Coregonus clupeaformis*); évaluation de l'habitat du poisson. Can. Tech. Rep. Fish. Aquat. Sci. 3110: vi + 40 p.

Les perturbations de l'habitat à grande échelle peuvent affecter la productivité des espèces de poissons importantes pour les pêches commerciales, récréatives et autochtones. Dans de nombreux cas, les changements à la productivité du poisson peuvent ne pas être décelés en raison de la difficulté à obtenir des estimations suffisamment solides de l'abondance de la population ou de la force de la classe d'âge sur une période donnée. En l'absence de mesures directes et solides de la productivité du poisson, l'élaboration et l'évaluation d'indicateurs biologiques, physiques et chimiques s'imposent en vue d'établir des liens entre la productivité du poisson et les perturbations de l'habitat. De tels indicateurs peuvent s'avérer utiles pour la prise de décisions relatives aux autorisations de perturber l'habitat en vertu de la législation et aux compensations de toute perte du point de vue de la productivité du poisson.

Cette étude avait pour but d'évaluer l'effet de l'eutrophisation et de l'abaissement du niveau d'eau en hiver sur l'habitat du grand corégone. L'eutrophisation expérimentale dans le nord-est du bassin du lac 226 (L226) dans la région des lacs expérimentaux survenue entre 1973 et 1980 a entraîné une réduction, et certaines années la disparition, de l'habitat idéal du grand corégone tel que défini par les besoins physiologiques de l'espèce au chapitre de la température (≤ 12 °C) et de l'oxygène dissous (≥ 4 mg/L). Ces changements sont principalement attribuables à l'eutrophisation du volume d'eau bien oxygénée dans l'hypolimnion et le métalimnion, plutôt que par les modifications à la profondeur de l'isoplèthe à 12 °C, qui est demeurée relativement stable. Le volume d'eau dans les conditions de température et d'oxygène dissous (OD) idéales pour le grand corégone (c.-à-d. l'habitat physiologique) a décliné plus rapidement après la stratification thermique dans le lac où a été menée l'eutrophisation expérimentale que dans le lac témoin. Par conséquent, le nombre de jours où l'habitat était modérément (< 10 % de l'habitat disponible) ou sévèrement (< 1 % de l'habitat disponible) inaccessible a augmenté d'environ 60 jours et 30 jours respectivement. Les effets de l'abaissement du niveau d'eau en hiver ont eu une incidence sur l'habitat du grand corégone en réduisant le volume d'eau correspondant aux exigences optimales de température et d'O_2. Bien que l'abaissement du niveau d'eau n'a pas eu d'incidence sur la production ou le transfert de matière organique, ou la demande en oxygène des sédiments, la diminution du volume hypolimnique a réduit l'habitat potentiel disponible total et a fait augmenter le taux d'appauvrissement en oxygène. Dans l'ensemble, le nombre de jours où l'habitat était modérément ou sévèrement inaccessible a augmenté de 44 jours et de 2 jours respectivement. Comme le régime alimentaire du grand corégone dépend principalement du benthos, la diminution de l'habitat physiologique idéal (c.-à-d. le volume du lac) a entraîné également une réduction de l'habitat d'alimentation idéal (zone au fond du lac où la température et l'OD sont optimales). Vraisemblablement, la diminution de l'habitat d'alimentation idéal renforcerait la compétition pour les ressources alimentaires, ferait augmenter le nombre de poissons en quête de nourriture à l'extérieur des conditions optimales, ou entraînerait une combinaison de ces deux conséquences, et mènerait à une diminution de l'état, de l'abondance et de la productivité du grand corégone.

INTRODUCTION

Amendments to the Canadian Fisheries Act (June 2012) focus on protection of the productivity of commercial, recreational and aboriginal (CRA) fisheries. However, assessments of fish productivity are both complicated and challenging, requiring extensive fish sampling at the beginning and end of the fishing season to estimate the change in fish biomass (i.e., productivity) at the individual or population level. Moreover, in order to determine the effect of habitat disruption on fish productivity, baseline fish productivity prior to the habitat disruption must be established, and data collection over multiple years (pre and post-disruption) may be required to differentiate changes in productivity caused by the disruption from natural variation. In order for the ecosystem approach to fisheries management to be meaningful, linkages between fish productivity and the food webs supporting them must be established. In addition, physical and chemical parameters that potentially affect fish production (e.g., deep-water hypoxia resulting from nutrient loading/eutrophication) need to be identified and included in decision making processes regarding approvals for habitat disruptions, and offsetting for potential losses to fish productivity. Because assessments of fish productivity, and changes in productivity, are methodologically challenging, ecosystem indicators of fish productivity (including potential physical and chemical parameters like those listed above) may provide a useful alternative to direct measurement. By tracing the indirect effects of habitat disturbance to parameters of interest (e.g., changes in fish productivity, influence on sensitive species) this analysis becomes highly relevant to ecosystem-based fisheries management.

Lake Whitefish are cold-water fish with a feeding preference for benthic macroinvertebrates in the profundal zone. Habitat disruptions such as eutrophication and reservoir drawdown can affect the productivity of cold-water fish, such as Lake Whitefish, in several important ways including: egg desiccation and/or freezing during drawdown, losses of optimal habitat for temperature and dissolved oxygen, and loss of habitat to access prey (i.e., benthic macroinvertebrates). In some studies (e.g., Plumb and Blanchfield 2009), optimal cold-water habitat is considered as the volume of water, or the proportion of lake volume, that meets a species' physiological requirements for temperature and oxygen. We refer to this aspect of fish habitat as 'optimal physiological habitat'. Assessments of available optimal physiological habitat are particularly useful for fish species that rely on pelagic prey, and can utilize the full extent of optimal habitat (i.e., volume) available. However, because Lake Whitefish are primarily benthivores, the effects of habitat disruption on losses of benthic area available for foraging must also be considered. We refer to this aspect as 'optimal foraging habitat', i.e., the total amount of benthic area, or the proportion of benthic area to total lake area, that occurs within the physiological optima (temperature and dissolved oxygen) for that species. The optimal physiological habitat and optimal foraging habitat are related measures, but are differentially affected by lake slope. In steep-sided lakes, effects on optimal physiological habitat and optimal foraging habitat will be similar, however as shoreline slope declines the magnitude of effects increasingly diverge.

Our objective is focused on evaluating the effect of two large habitat manipulations (i.e., eutrophication and water level drawdown) on the availability of optimal physiological and foraging habitat for Lake Whitefish, and other cool water species, because these factors are expected to influence mortality, productivity, and reproductive success (Figs. 1 and 2). While our efforts focus on the effects of large-scale ecosystem manipulations on the optimal habitat for Lake Whitefish as a model, similar effects would be expected for the habitat of other cool water species.

METHODS

We used pre-existing datasets from two whole-ecosystem experiments conducted at the Experimental Lakes Area (ELA) to evaluate the effects of artificial nutrient enrichment (eutrophication) and winter water-level drawdown (simulating effects of hydroelectric development) on the thermal and dissolved oxygen (DO) requirements of Lake Whitefish.

Study site

Lake 226 is a small (16.1 ha, Fig. 3) two-basin lake located on the Pre-Cambrian shield in the boreal forest of Ontario at the ELA (Cleugh and Hauser 1971). The ELA is located in a sparsely inhabited remote region of northwestern Ontario, Canada that is relatively unaffected by external human influences and industrial activities. Lake 226 is naturally oligotrophic-mesotrophic and has a cold-water fish community consisting primarily of Lake Whitefish (*Coregonus clupeaformis*), Fathead Minnow (*Pimephales promelas*), Northern Pearl Dace (*Margariscus nachtriebi*), Northern Redbelly Dace (*Chrosomus eos*), Finescale Dace (*Chrosomus neogaeus*) and Slimy Sculpin (*Cottus cognatus*). Lake Whitefish is an ecologically and economically important cold-water fish of the Salmonidae family that move from shallow to deep water as lake warming and thermal stratification occurs (i.e., during early summer), then back to shallow water in the cooler months. Lake Whitefish spawn from September through December, usually in shallow water 2 – 4.5 m deep, and lay their eggs over sand, gravel, flat stone, cobble and boulder (Dubois and Dziedzic 1989, Dumont and Fortin 1978, Fudge and Bodaly 1984, Hart 1930, Nester and Poe 1984). The larval and postlarval stages feed on zooplankton. Once the larvae reach about 76-100 mm in length, they switch to feeding on bottom-dwelling organisms including small fishes, fish eggs, amphipods, aquatic insect larvae, clams, snails and plankton.

Experimental manipulations

We focus our current effort on two whole-ecosystem experiments that occurred at different times in Lake 226: a eutrophication experiment where phosphorus (P), nitrogen (N), and carbon (C) were added to the northeast basin (NE) for 8 years, while the southwest (SW) only received N and C; and a lake drawdown experiment (to simulate overwinter water removals occurring in reservoirs associated with hydro-electric generating stations) over three successive winters.

The eutrophication experiment was carried out from 1973 to 1980. A vinyl sea curtain was installed in June 1973 to isolate the NE basin (8.3 ha, 14.7 Z_{max}) from the SW basin (7.8 ha, 11.6 m Z_{max}) and remained in place until July 1985. Leakage of the vinyl curtain occurred in 1977, 1978 and 1980; however, the effect of this leakage on the migration of fish and nutrient exchange between the basins was minimal (Mills and Chalanchuk 1987). Both basins received N (NE 1.81 $g \cdot m^{-2} \cdot yr^{-1}$ and SW 1.93 $g \cdot m^{-2} \cdot yr^{-1}$) and C (NE 3.46 $g \cdot m^{-2} \cdot yr^{-1}$ and SW 3.69 $g \cdot m^{-2} \cdot yr^{-1}$) additions during the ice-free periods from 1973 to 1980, and the NE basin also received P additions (0.34 $g \cdot m^{-2} \cdot yr^{-1}$) during the same period. Blue-green algal blooms occurred each year of fertilization in the NE basin (which received C+N+P), but not in the SW basin (which received only C+N) (Findlay and Kasian 1987). The NE basin also had higher primary productivity, phytoplankton biomass and dipteran emergence than in the SW basin (Davies 1980, Findlay and Kasian 1987, Shearer et al. 1987, Schindler 1974, Schindler and Fee 1974). Following cessation of nutrient additions, phytoplankton biomass decreased to levels observed prior to fertilization.

A decade after the eutrophication experiment and removal of the sea curtain, the water level of Lake 226 was lowered for three successive winters (1994/95 to 1996/97) to simulate winter drawdown of larger reservoirs. Drawdown started in December of each winter and was completed by February of the following year. The natural outflow channel was modified to allow a drawdown of 2 m in the winter of 1994/95 and large siphons were used to supplement this drawdown to 3 m in the winters of 1995/96 and 1996/97. The water level recovery by spring melt and rain runoff during the remainder of each year varied from 25% to more than 80% (Mills et al. 2002a), which is typical of many Canadian reservoirs (Rosenberg et al. 1987). The water level of Lake 226 returned to pre-drawdown values during spring snow-melt in 1998.

Fish sampling

All sampling and processing procedures were selected to minimize mortality of Lake Whitefish (Mills 1985). Briefly, Lake Whitefish were captured in the midmorning (08:00 – 10:30) in May and from September to October using small-mesh (9.5 mm) deep-water trap nets (Beamish 1972). Trap net catches were supplemented with multi-panel gill nets (11-, 25-, 30-, 33-, 38- and 45-mm bar mesh) commencing in September 1975 because trap net catch-per-unit-effort (CPUE) decreased at this time. Gill nets were emptied at 15-minute intervals to minimize mortality. Captured Lake Whitefish were anesthetized with MS-222® (tricaine methane sulfonate) and weighed, measured (fork length) and sexed by extrusion of gametes (October). Fish were batch-marked by systematically clipping two to three rays from different fins corresponding to individual sampling periods and then tagged with either Floy® gun tags (Dell 1968) or Carlin tags (White and Beamish 1972). The first two to three fin rays were removed from the left pelvic fin at initial tagging for age determination.

Water chemistry timeframe selection

Chlorophyll-*a* (chl-*a*), suspended phosphorus (Susp P) and total dissolved phosphorus (TDP) were sampled bi-weekly during the ice-free season from 1973 to 1995, with the exception of 1987 and 1994 in the NE basin and 1984, 1987 and 1994 in the SW basin, which were sampled monthly. Water chemistry was also sampled monthly in years 1996, 1997, 2001, 2002, 2003 and 2004 in the NE basin and in 1996, 1997, 2002 and 2003 in the SW basin. Only chl-*a* was sampled in 1983.

The majority of sampling occurred between Julian dates 121-304 (May 1 – Oct 31). The ability to predict the annual averages of Chl-*a*, Susp P and TDP was assessed by regressing the average concentrations of all available samples collected within the sampling timeframe against the average concentration of all samples collected within a given year.

Whitefish Habitat Constraint

Temperature and dissolved oxygen profiles were measured approximately bi-weekly during the ice-free season. Dissolved oxygen was sampled less frequently in the winter and only in years 1974 to 1981.

Lake Whitefish are a cold-water fish that prefer dissolved oxygen concentrations above 4 mg/L (Davison et al. 1959). While many laboratory-based studies suggest Lake Whitefish prefer temperatures between 12 °C and 19.5 °C (Bernatchez and Dodson 1985, Edsall 1999a, b, Ferguson 1958, Hoagman 1974, Jobling 1981, Tompkins and Fraser 1950) field observations suggest that Lake Whitefish primarily occupy temperatures below 12 °C (Cooper and Fuller 1945, Madenjian et al. 2006). This difference between laboratory-based temperature preference and field observations of Lake Whitefish may be attributed to age differences since laboratory studies are conducted on young fish and field observations are generally made on older fish (Ferguson 1958). Moreover, the acclimation temperature used in these laboratory studies can significantly affect derived preferred temperatures (Ferguson 1958, Fry 1947), which may account for the wide range in laboratory-derived Lake Whitefish preferred temperatures. Given this influence of age and acclimation temperature on laboratory-based preferred temperatures, the field observation-based temperature of less than 12 °C was used to represent the optimal thermal habitat for Lake Whitefish in this study.

Optimal Lake Whitefish habitat preference was calculated for each sampling event by assessing the depths where the temperature was < 12 °C and the dissolved oxygen was >4 mg/L and adjusting for the water level change respective to the benchmark of 8.5 m. The area of lake bottom and the pelagic volume within each depth contour were calculated from hypsographic curves and used to assess the area and volume that represented optimal habitat in terms of thermal and DO preferences.

In several years, temperature sampling commenced after the surface water temperature of Lake 226 had reached 12 °C (NE and SW basins: 1979, 1981, 1984, 1985, 1987, 1988, 1989, 1991, 1993, 1996, and 1998; SW basin only: 2003). For these years, the date was estimated by comparing the Julian date where the lake surface reached 12 °C in reference Lake 239 with that of dates in Lake 226 where this information was available (n = 17). On average, the surface of Lake 239 reached 12 °C nine days earlier than that of Lake 226. Therefore, for the years stated above, the Julian date where the lake surface reaches 12 °C was calculated by subtracting nine days from the Julian date where the surface of Lake 239 reached 12 °C.

Water temperatures were not sampled in several years (NE and SW basins: 1999, 2000, 2001, 2005 and 2006; SW basin only: 2004). The average depths where the temperature equaled 12 °C from 1986 to 1994 were used for these years. Similarly, the dissolved oxygen was not measured in several years (NE and SW basins: 1991, 1992, 1993, 2000, 2001, 2002, 2003, 2004, 2005 and 2006; NE basin only: 1998; SW basin only: 1999). The average depths were the dissolved oxygen equaled 4 mg/L from 1988 to 1990 were used for these years.

For statistical tests, data from 1991, 1992 and 1993 were not considered in the pre-manipulation data set for the lake drawdown experiment, since the dissolved oxygen profiles in these years were modeled from dissolved oxygen data from 1988 to 1990.

RESULTS

Water Chemistry

Chl-*a* was not sampled in 1998, 1999 and 2000, and was limited in 1983: The SW basin was sampled for dissolved oxygen in the winter (1/10/83, 2/14/83, and 3/13/83) and chl-*a* (n = 6). The NE basin was only sampled for chl-*a* (n = 6) and neither basin was sampled for Susp P and TDP. The majority of sampling occurred between Julian dates 121-304 (May 1 – Oct 31, Fig. 4). Regression analyses (Table 1, Fig. 5) reveal that the Julian dates 121-304 timeframe adequately predicted the annual average concentrations (i.e., all samples collected within a year). While the slopes of the regressions are significantly different than 1 (Table 1), the Julian dates 121-304 averages only overestimated the chl-*a*, Susp P and TDP annual averages by 3.3 ± 13.1%, 5.9 ± 6.5% and 1.6 ± 4.5%, respectively. The Julian dates 121-304 averages overestimated the annual chl-*a* concentrations above 9 μg/L by 10.8 ± 8.4% and Susp P concentrations above 8 μg/L by 9.9 ± 6.1%. The Julian dates 121-304 were therefore deemed sufficient and were used for the yearly averages of chl-*a*, Susp P and TDP.

During the eutrophication years (i.e., 1973 to 1980), chl-*a* concentrations were higher in the NE basin than in the SW basin (Fig. 7, $p<0.01$, Table 2) and steadily increased during the summer months in the NE basin, reaching maximum concentrations around Julian date 242 ± 28 days (Fig. 6). The distribution of chl-*a*, Susp P and TDP concentrations throughout the sampling years (i.e., 1973 to 2008) are available in Figure 7. The highest concentrations of Chl-*a*, Susp P and TDP occurred during the years of the eutrophication experiment (Figs. 7, $p<0.01$, Table 2).

The water level drawdown experiment resulted in a slight increase in Chl-*a* concentrations (Fig. 7, $p<0.05$, Table 2).

Whitefish Habitat Constraint

On average, the depth of the 12 °C isothermal reached its maximum around Julian dates 260 ± 7 days and 259 ± 10 days in the NE basin and SW basin, respectively (Figs. 8-13). Winter dissolved oxygen sampling occurred only in years 1974 to 1981. Given that the majority of the water column was hypoxic in the NE basin in each winter from 1974 to 1981 (Figs. 9-11), the optimal foraging and physiological habitats were only capable of being calculated for the Julian dates 121-304 timeframe for years post-1981. During the winter months in 1978 and 1979, the dissolved oxygen depletion (Fig. 10) was severe enough to reduce the optimal foraging and physiological habitats to less than 10% of the total lake area and volume, respectively (Fig. 16).

The 4 mg/L DO isopleth reached its shallowest depths towards the end of the stratified period (i.e. Julian date 232 ± 16 days). The 'shallowing' of the DO isopleth is particularly detrimental if it crosses (i.e. becomes shallower than) the 12 °C thermal isopleth, which deepens through the stratified period. Such a circumstance would indicate that there were no refuge in the ecosystem where thermal and DO requirements were optimal for Lake Whitefish. In all years, the isopleths representing optimal thermal and DO concentrations converged during the stratified period and optimal foraging and physiological habitat were most constricted during late summer, between Julian dates 220 to 270 (Figs. 14-16). Optimal foraging and physiological habitats were constricted (< 1, 5 or 10% of total lake area and volume) for the longest duration in the NE basin, which received phosphorus additions, during the years of the eutrophication experiment (i.e., 1973 to 1980, Figs. 14-16, $p<0.05$, Table 2) and were more constricted in the NE basin than in the SW basin (Figs. 16-17, $p<0.01$, Table 2). During the eutrophication experiment (i.e., 1973 to 1980), the availability of optimal foraging and physiological habitats fell below 10% of the lake area and volume, respectively, in the NE basin for, on average, 22.9 ± 6.6% and 19.4 ± 4.6% of the year, respectively, compared to the SW basin, which only fell below 10% lake area and volume for 6.2 ± 9.6% and 5.1 ± 5.7%, respectively. In 1978 and 1979, Lake Whitefish were subjected to sub-optimal foraging habitat (<10%) for 31.2% and 31.0% of the year, respectively. Constriction of optimal foraging and physiological habitats were due to deep-water hypoxia encroachment into shallower depths (Figs. 9, 10 and 18). Minimum depths of dissolved oxygen in the NE basin were shallower than those in the SW basin during the eutrophication experiment (Figs. 9, 10, 18 $p<0.01$, Table 2) and were correlated with Chl-*a* concentrations (Fig. 19, $p<0.01$, Table 2).

While water level drawdown did not alter the thickness of the epilimnion, mean reductions in hypolimnetic thickness (between 1-2 m) and volume occurred during the stratified period. Thus, relative to the pre-drawdown benchmark, the depth of the 12 °C isopleth increased (i.e. became 'deeper') leading to a reduction in the optimal foraging and physiological habitats for Lake Whitefish (Fig 2). The water level drawdown that occurred each winter from 1994/1995 to 1996/1997 affected the optimal foraging and physiological habitats (Figs. 15, 16). The optimal foraging and physiological habitats were constricted to less than 5 and 10% for a longer duration during the water level drawdown years (i.e., 1995 to 1997) than in years preceding the manipulation (i.e., 1989, 1990 and 1994, $p<0.01$, Table 2).

DISCUSSION

Eutrophication effects

Our results indicated that the primary effect of eutrophication on optimal Lake Whitefish habitat resulted from an increased depletion rate of DO in the hypolimion and metalimion of

L226 resulting from increased sediment oxygen demand (SOD) rather than potential changes to the thermal structure and concomitant effects on hypolimnetic volume. While the 12 °C isopleth continually increased in depth (i.e. became deeper) throughout the stratified period, such patterns are common in lakes and there was no difference between experimental and control basins. However, increased SOD resulting from the increase in organic matter deposition reduced DO concentrations in the water overlaying the hypolimnetic sediments. As the stratified period progressed, the depth of the 4 mg/L DO isopleth became shallower and the volume of water considered to represent optimal physiological habitat for Lake Whitefish was either reduced substantially or completely eliminated. Overall, the effect of eutrophication significantly reduced the time period where ≥10% of the lake volume was considered optimal habitat by nearly 60 days, and the time period where ≥1% of lake volume was considered optimal by approximately 30 days.

As noted elsewhere (e.g. Dillon et al. 2003, Evans et al. 1991, Molot et al. 1992, Plumb and Blanchfield 2009) optimal foraging and physiological habitats in our study were most frequently constricted between towards the end of the summer stratified period, or immediately prior to ice-off. Therefore, it is recommended that the measurement of minimal habitat availability occur during these timeframes and at a minimum include the sampling of temperature, dissolved oxygen and chl-*a* (Table 3). Dissolved oxygen depletion that occurred each winter during the eutrophication experiment (i.e., 1973 to 1980) suggests that sampling programs that assess the effects of eutrophication should include winter sampling of dissolved oxygen. During the eutrophication experiment, winter dissolved oxygen depletion of the water column generally occurred between Julian dates 40 to 94 (i.e., 9 February to 4 April) and therefore it is recommended that this timeframe be included in the measurement of minimal under-ice habitat availability, particularly if effects of eutrophication are being assessed.

Benthic invertebrates typically form the majority of Lake Whitefish diets, though they may also feed on zooplankton (Carl and McGuiness 2006, Rennie et al. 2012). The analysis of stomach contents of Lake Whitefish sampled from Lake 226 revealed diets primarily consisting of chironomids and chaoborids (Mills 1985). Because of the strong association with the lake bottom, a measure of estimated optimal habitat area within the 12 °C and 4 mg/L DO isopleths is likely a better indicator of optimal foraging habitat than estimated optimal habitat volume. Thus, while fish productivity is often positively correlated with primary productivity in lakes (Downing et al. 1990) due to increased pelagic food supply, the estimated optimal habitat area may be a better indicator of Lake Whitefish productivity due to its preference for benthic macroinvertebrates rather than pelagic plankton. Indeed, Christie and Regier (1988) found that estimated habitat area, based on temperature profiles alone, were a better predictor of Lake Whitefish sustained yield than the estimated habitat volume.

We suspect that the effect of eutrophication on optimal foraging habitat availability for Lake Whitefish will correlate with changes in Lake Whitefish productivity. Temperature and dissolved oxygen profiles have been shown to be suitable estimates of habitat occupied by other cold-water fish species, such as Lake Trout (*Salvelinus namaycush*), that share similar physiological requirements with Lake Whitefish (Plumb and Blanchfield 2009). For example, Plumb and Blanchfield (2009) found that the habitat area and volumes occupied by Lake Trout in an ELA lake closely matched the physiologically optimal habitat available to fish within temperature and dissolved oxygen constraints. The availability of habitat that is physiologically optimal for Lake Whitefish can contribute to the productive capacity of fish populations (Christie and Regier 1988). A strong positive correlation was found between Lake Whitefish yield and the available thermal habitat area and volume in several lakes throughout Canada (Christie and Regier 1988). Therefore, it is probable that the productivity of the Lake Whitefish population would decline during sustained periods of restriction of Lake Whitefish habitat area and volume.

Water level drawdown effects

The optimal foraging and physiological habitats were influenced by winter water level drawdown, albeit to a lesser extent than with eutrophication. During years of water level drawdown, water levels recovered from 25% to more than 80% of pre-drawdown levels by spring-melt (Mills et al. 2002a), However, water levels remained approximately 1-2 meters below pre-drawdown levels at the initiation of the stratified period. As a result, because the thickness of the epilimnion remained relatively constant, the combined thickness of the metalimnion and hypolimnion, and that below the 12 °C isopleth, was reduced by 1-2 meters.

The change in the optimal foraging and physiological habitats associated with water-level drawdown also resulted from a shallowing of the 4 mg/L dissolved oxygen depth (Fig. 18). However, annual variation in deepwater DO concentrations, resulting from incomplete lake-turnover during the spring period, make it difficult to distinguish whether the shallowing of the 4mg/L DO isopleth is a result of the experimental manipulation or simply natural variation.

Mills et al. (2002a) found a decrease in Lake Whitefish abundance as well as recruitment failures during the water level drawdown experiment in Lake 226. A telemetry study conducted by Bégout-Anras et al. (1999) revealed that adult Lake Whitefish spawned in the nearshore of Lake 226 from October to November, which corresponded to the areas within the drawdown zone in Lake 226. Therefore, the recruitment failures witnessed during the water level drawdown experiment in Lake 226, which occurred from December to February, were likely due to the desiccation and/or freezing of Lake Whitefish eggs, which would impact Lake Whitefish productivity. The condition of individual Lake Whitefish progressively increased during the water level drawdown experiment (Mills et al. 2002a), suggesting a decrease in intraspecific competition and negligible effects of alterations to the physiological or foraging habitat on the productivity of adult Lake Whitefish.

ACKNOWLEDGEMENTS

This study was funded by the Strategic Program for Ecosystem-based Research and Advice (SPERA). We thank the ELA staff members who conducted the experimental manipulations; David Schindler, Drew Bodaly and Mark Lyng who managed the lake sampling in Lake 226; Ken Mills, Sandy Chalanchuk and Doug Allan whom collected countless fish over many seasons from Lake 226; and Ken Beaty who designed and operated the drawdown experiment in Lake 226. We would also like to thank Doug Guss for his assistance with the Oracle database. We gratefully acknowledge Patricia Ramlal, Bob Randall and Doug Watkinson for their helpful reviews of this manuscript.

TABLES

Table 1. Results of regression analysis between annual averages and averages within Julian dates 121 to 304 from 1973 to 2006.

	Chl-a	Susp P	TDP
	y=0.78x+1.6	y=0.85x+0.83	y=0.93x+0.24
R^2	0.95	0.99	0.98
p-value	<0.0001	<0.0001	<0.0001
(*df*), *F*-ratio	(1,18), 307.1	(1,18), 1502	(1,18), 932.1
Slope different than 1?	Y, *p*<0.0001	Y, *p*<0.0001	Y, *p*=0.01
Intercept different than 0?	Y, *p*=0.003	N, *p*=0.005	N, *p*=0.09

Table 2. Results of various t-test comparisons.

Comparisons	*t*	*df*	*p*-value
Chl-*a* (NEB v SWB, 1973-1980)	6.1	11.1	<0.01
Chl-*a* (1973-1980 v 1981-1997)	10.8	7.6	<0.01
Chl-*a* (1989, 1990, 1994 v 1995-1997)	-2.0	111	<0.05
Susp P (1973-1980 v 1981-1997)	7.6	7.4	<0.01
TDP (1973-1980 v 1981-1997)	6.5	20.2	<0.01
Area <1% (NEB v SWB, 1973-1980)	5.7	11.2	<0.01
Area <5% (NEB v SWB, 1973-1980)	5.7	14.0	<0.01
Area <10% (NEB v SWB, 1973-1980)	4.1	12.4	<0.01
Volume <1% (NEB v SWB, 1973-1980)	5.0	8.6	<0.01
Volume <5% (NEB v SWB, 1973-1980)	6.5	13.1	<0.01
Volume <10% (NEB v SWB, 1973-1980)	5.6	13.4	<0.01
Area <1% (1989, 1990, 1994 v 1995-1997)	-1.7	5.3	>0.05
Area <5% (1989, 1990, 1994 v 1995-1997)	-3.3	10.0	<0.01
Area <10% (1989, 1990, 1994 v 1995-1997)	-4.4	10.0	<0.01
Volume <1% (1989, 1990, 1994 v 1995-1997)	-1.4	5.1	>0.05
Volume <5% (1989, 1990, 1994 v 1995-1997)	-4.2	5.7	<0.01
Volume <10% (1989, 1990, 1994 v 1995-1997)	-5.5	8.7	<0.01
Area <1% (NEB 1973-1980 v NEB 1981-1990, 1994)	3.4	16.0	<0.01
Area <5% (NEB 1973-1980 v NEB 1981-1990, 1994)	3.8	15.8	<0.01
Area <10% (NEB 1973-1980 v NEB 1981-1990, 1994)	2.3	14.4	<0.05
Volume <1% (NEB 1973-1980 v NEB 1981-1990, 1994)	2.9	15.7	<0.01
Volume <5% (NEB 1973-1980 v NEB 1981-1990, 1994)	4.2	14.7	<0.01
Volume <10% (NEB 1973-1980 v NEB 1981-1990, 1994)	2.7	15.6	<0.05

Table 3. Suggested sampling period and the minimum sampling variables that should be collected within each sampling period to assess minimal habitat availability for cold-water fish.

Sampling period (Julian dates)	Sampling variables
40-94 220-270	Lake morphometry chlorophyll-*a* Temperature profile dissolved oxygen profile

FIGURES

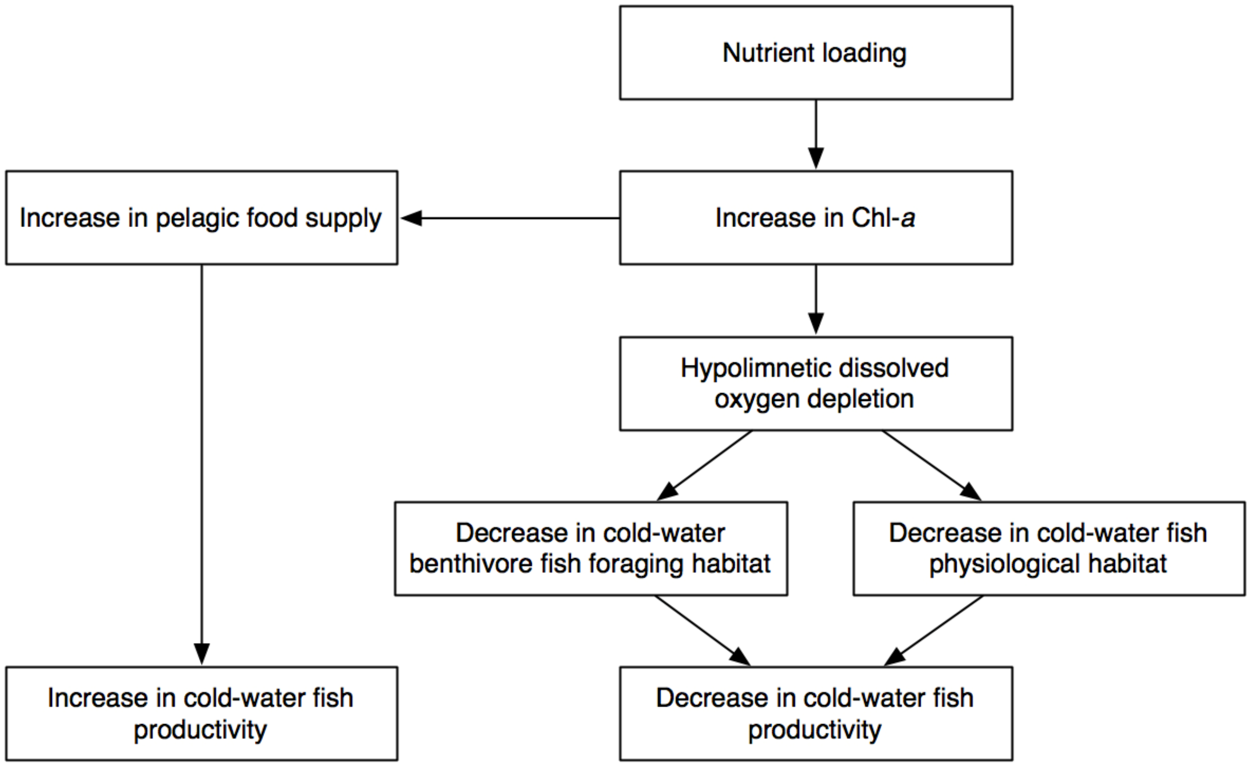

Figure 1. Pathway of effects of nutrient loading on cold-water fish productivity.

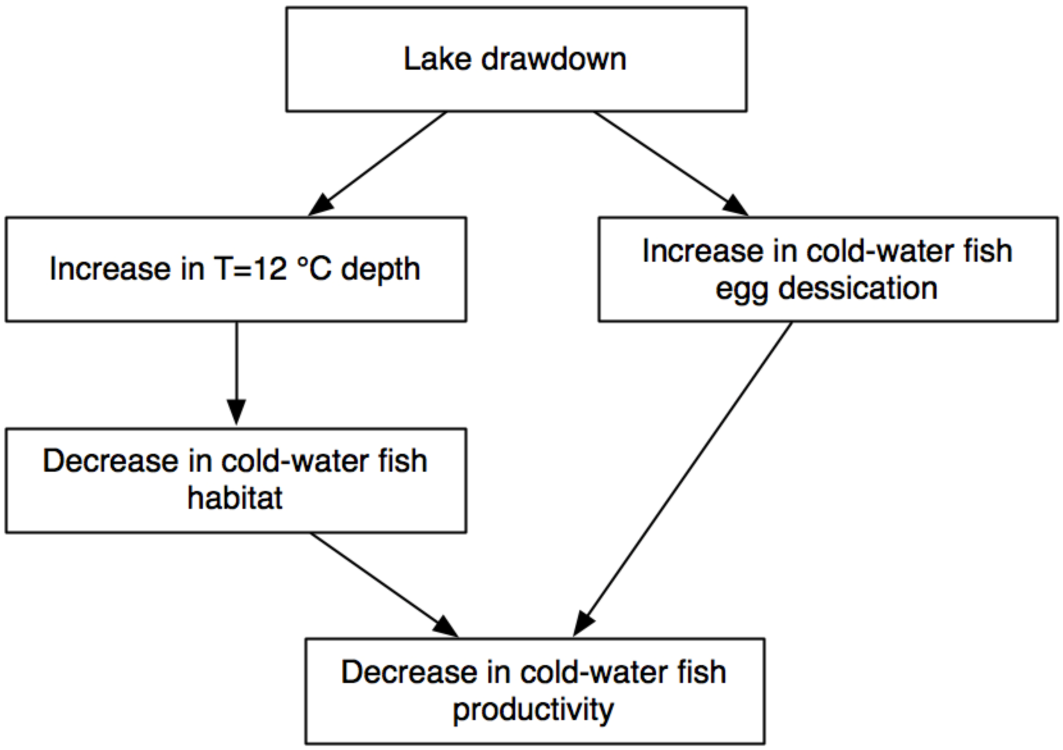

Figure 2. Pathway of effects of lake drawdown on cold-water fish productivity.

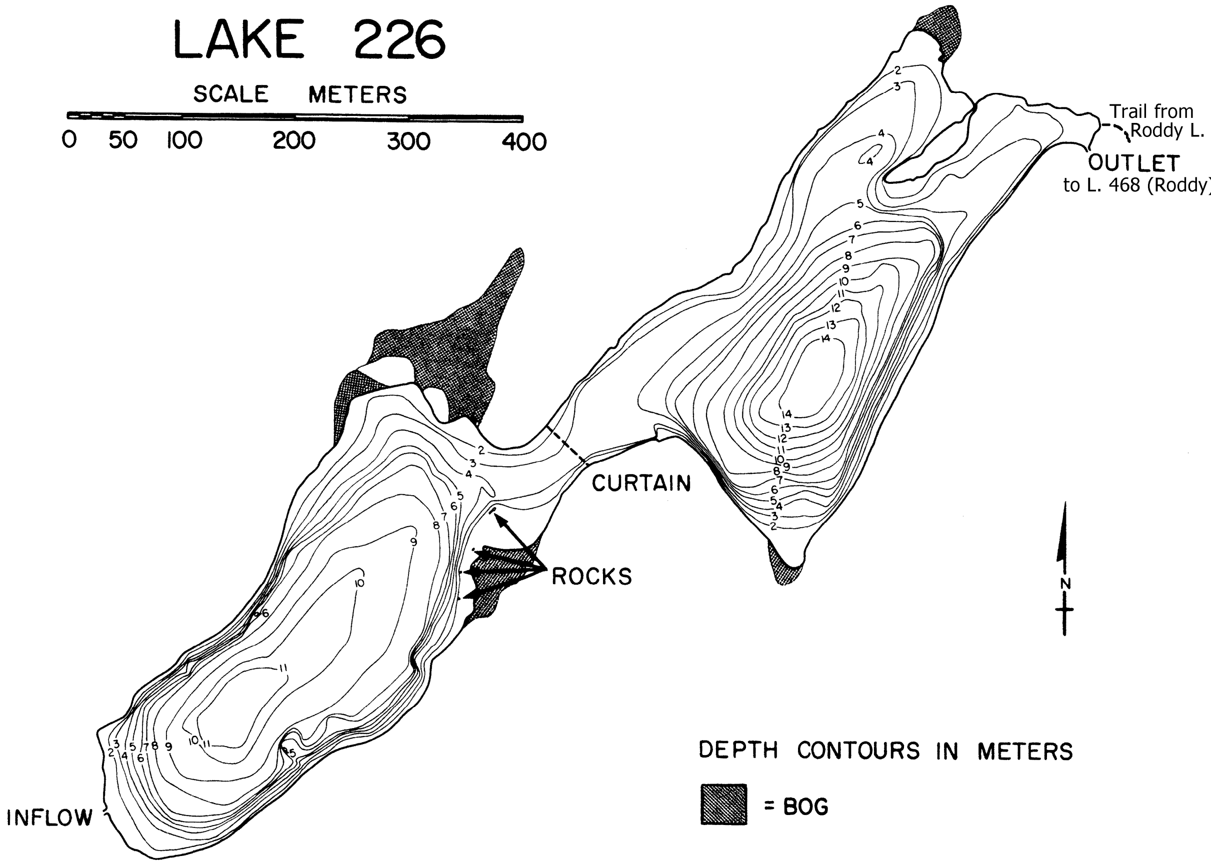

Figure 3. Bathymetric map at 1-m intervals of experimental Lake 226, northwestern Ontario, Canada.

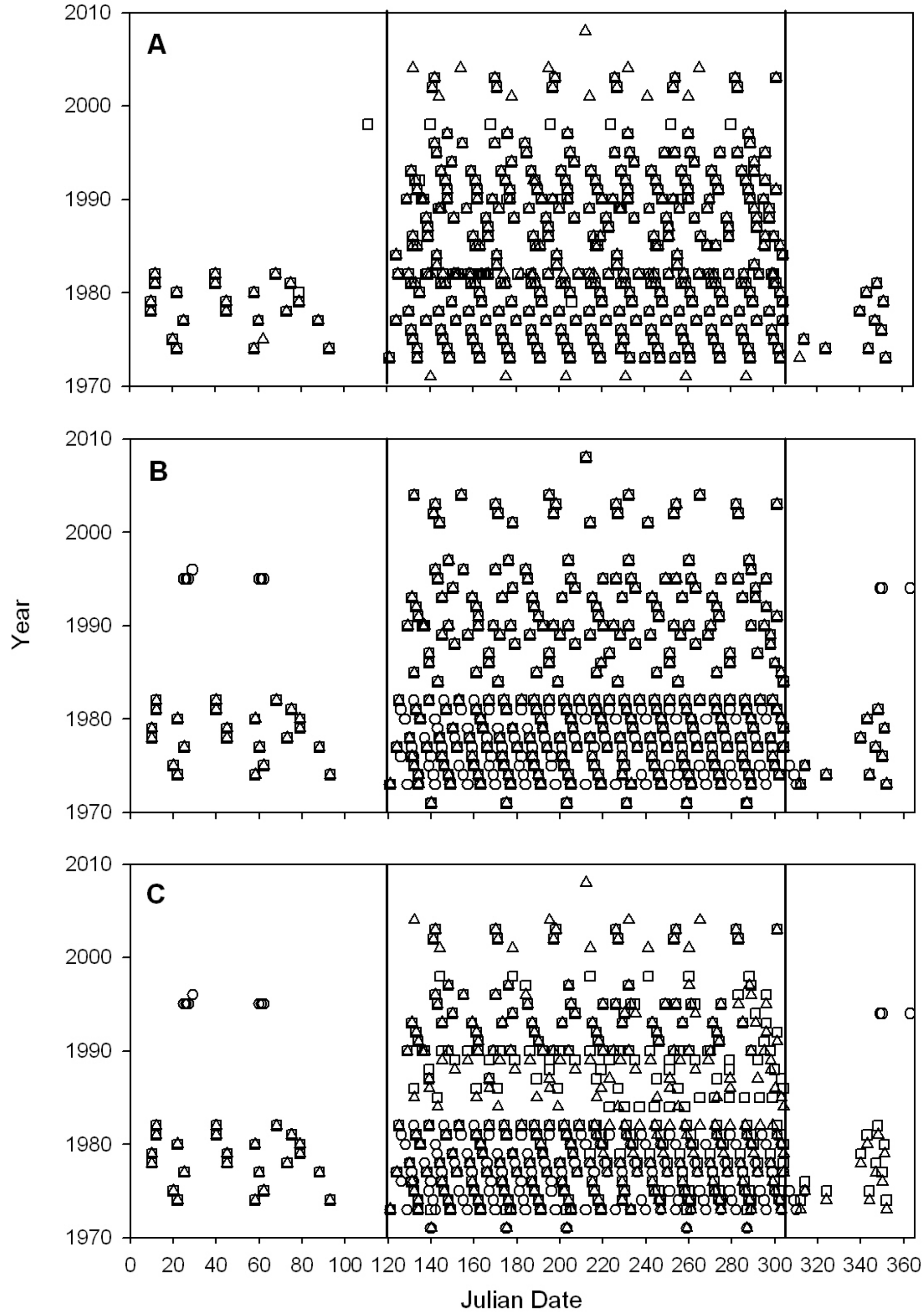

Figure 4. Seasonal distribution of sampling for Chl-*a* (A), Susp P (B) and TDP (C) in Lake 226 in the northeast basin (Δ), the southwest basin (□) and with the curtain removed (O). The vertical lines highlight the timeframe (i.e., ice-free period, Julian dates 121 to 304) that was selected to represent annual concentrations.

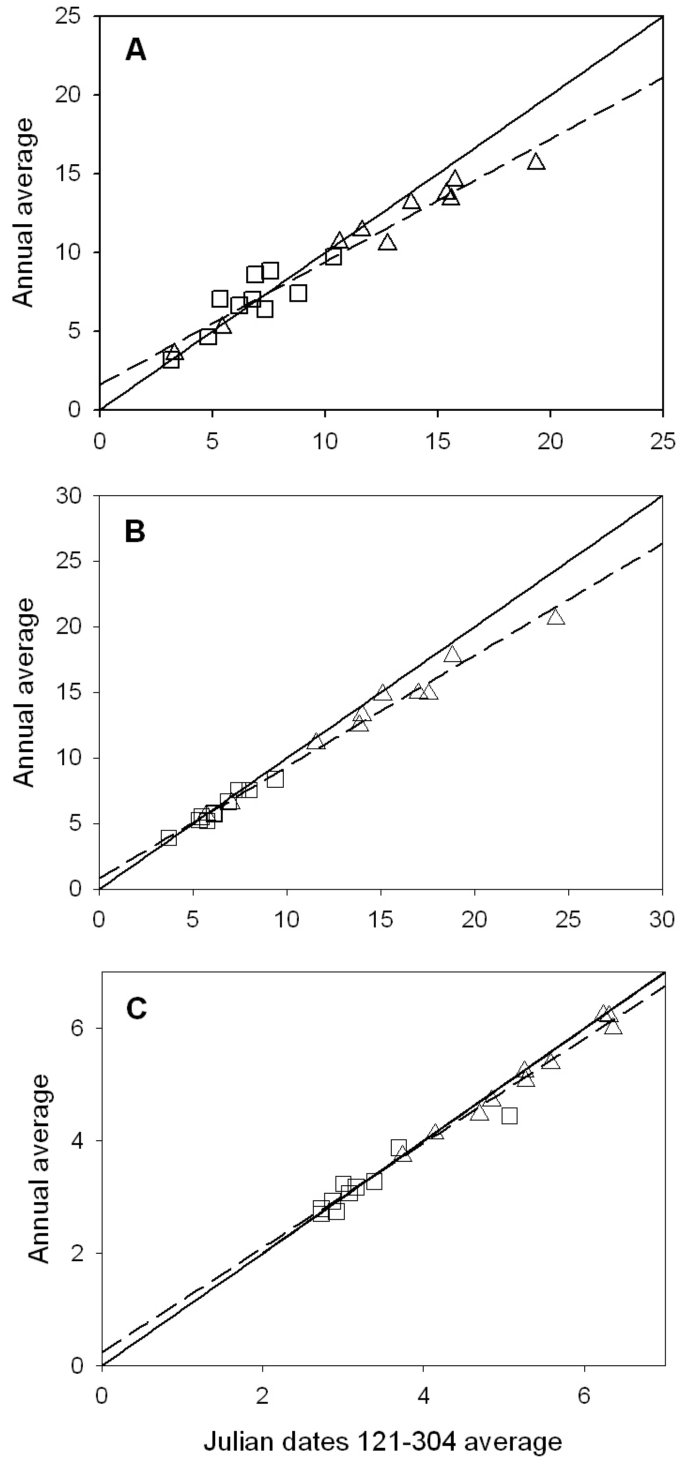

Figure 5. Comparison of Chl-*a* (µg/L, A), Susp P (µg/L, B) and TDP (µg/L, C) concentrations in the northeast basin (Δ) and southwest basin (□) averaged between Julian days 121-304 and compared to the annual average (i.e., all samples taken in a given year) from 1973 to 2006.

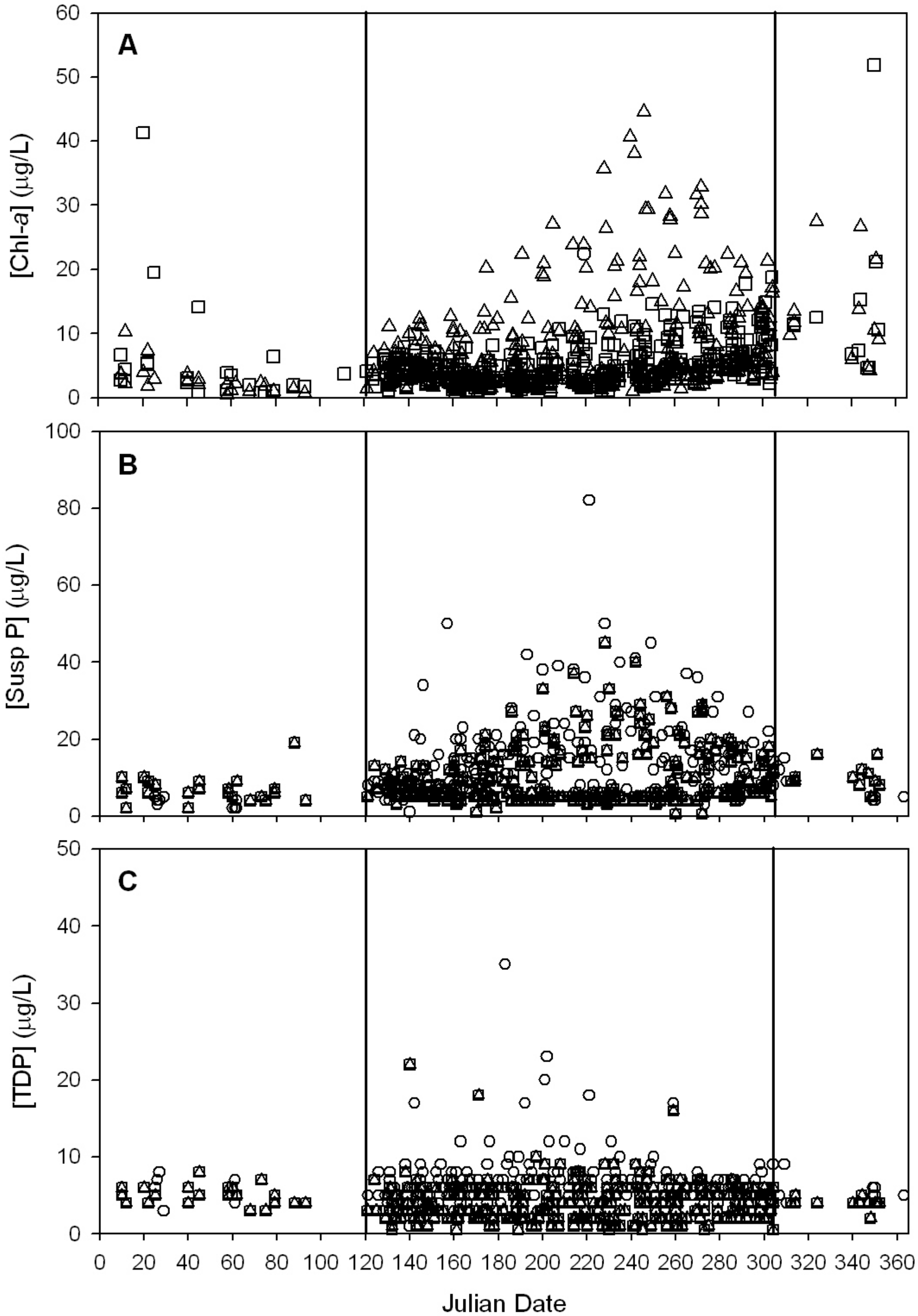

Figure 6. Seasonal distribution of Chl-*a* (A), Susp P (B) and TDP (C) concentrations in the northeast basin (Δ), the southwest basin (□) and with the curtain removed (○) across all sampling years (e.g., 1973 to 2008). The vertical lines highlight the timeframe (i.e., ice-free period, Julian dates 121 to 304) that was selected to represent annual concentrations.

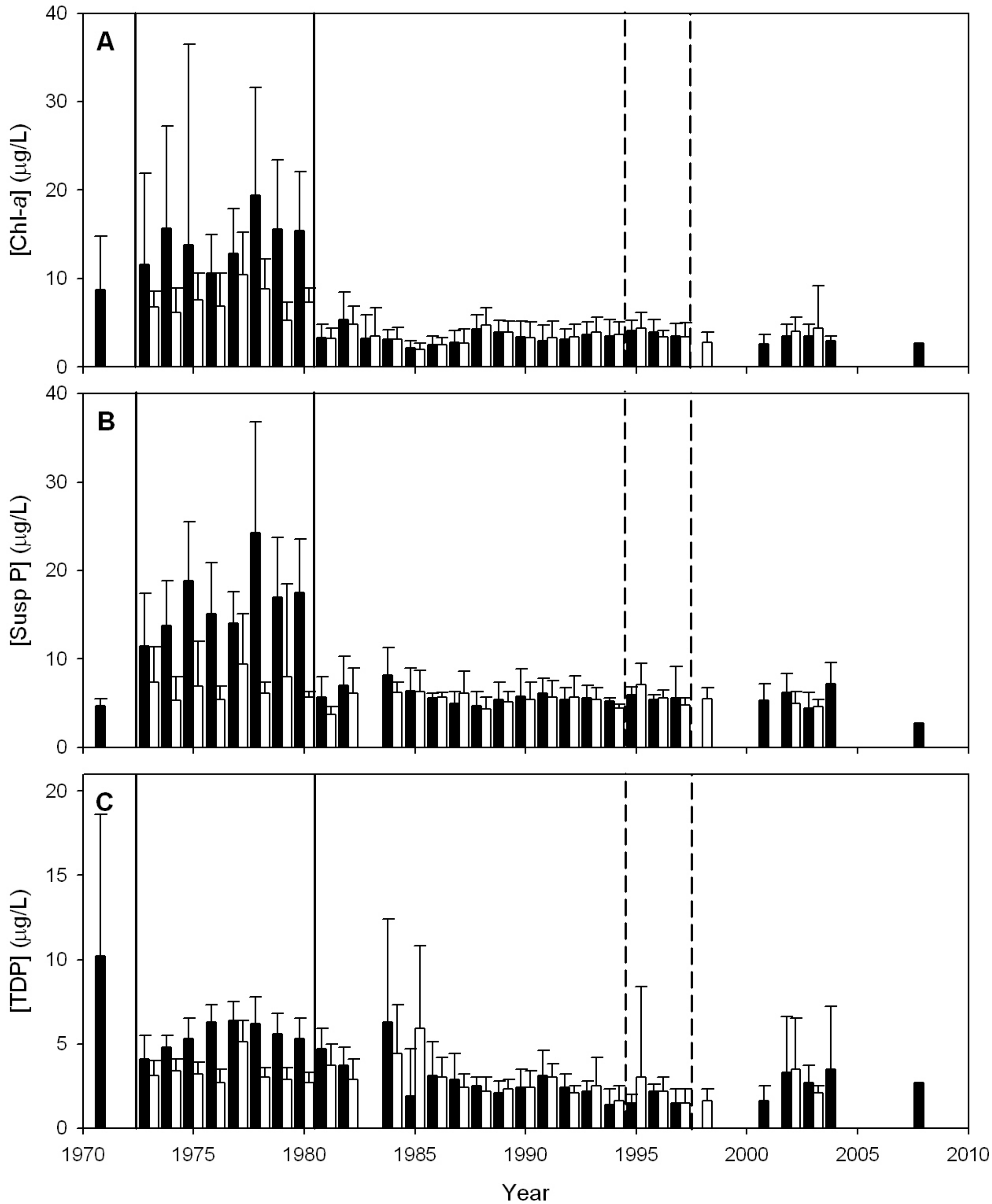

Figure 7. Average concentrations (± SD) of Chl-*a* (A), Susp P (B) and TDP (C) in the northeast basin (black) and the southwest basin (white) within the Julian date 121 to 304 timeframe throughout the sampling years 1973 to 2008. Years within the vertical solid and dashed lines represent the years of the eutrophication and water level drawdown experiments, respectively.

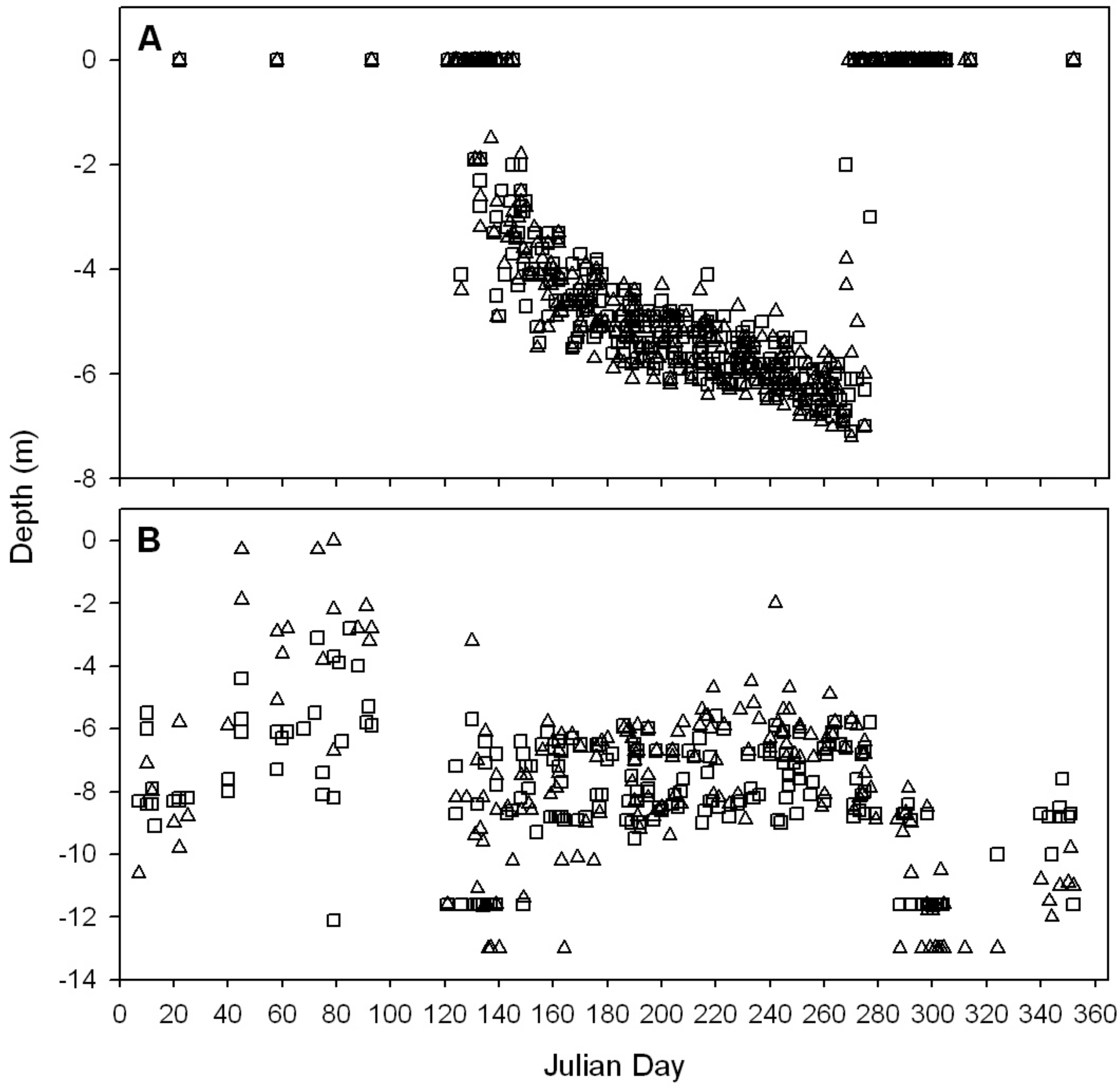

Figure 8. The seasonal distribution of the depth at which the temperature equals 12 °C (A) and the depth where the dissolved oxygen equals 4 mg/L (B) sampled from Lake 226 in the northeast basin (Δ) and in the southwest basin (□) from 1973 to 2006.

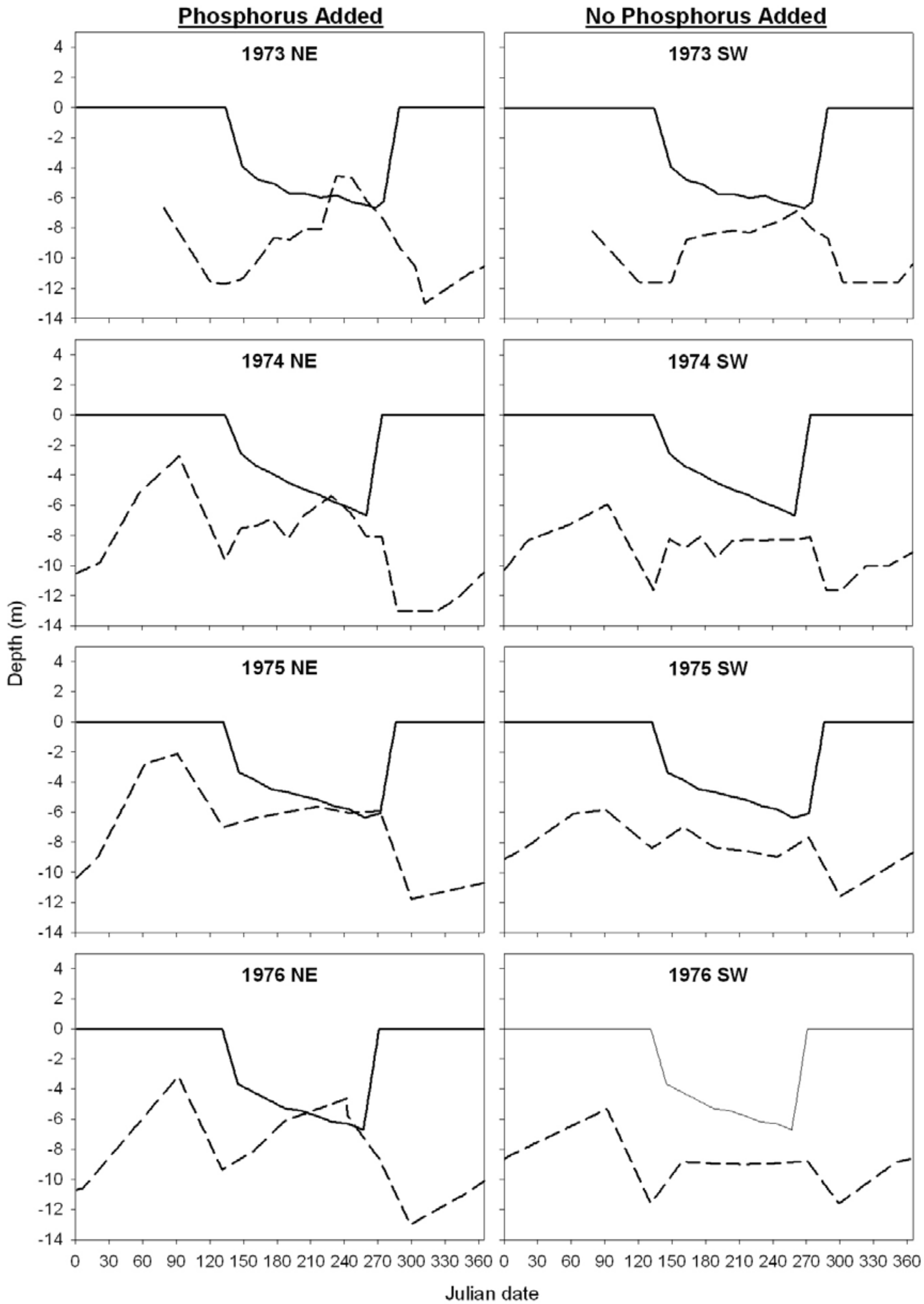

Figure 9. The daily interpolated depth where the temperature is ≤12 °C (solid line) and dissolved oxygen concentration of 4 mg/L (dashed line) in the northeast basin (NE) and the southwest basin (SW) during the eutrophication experiment.

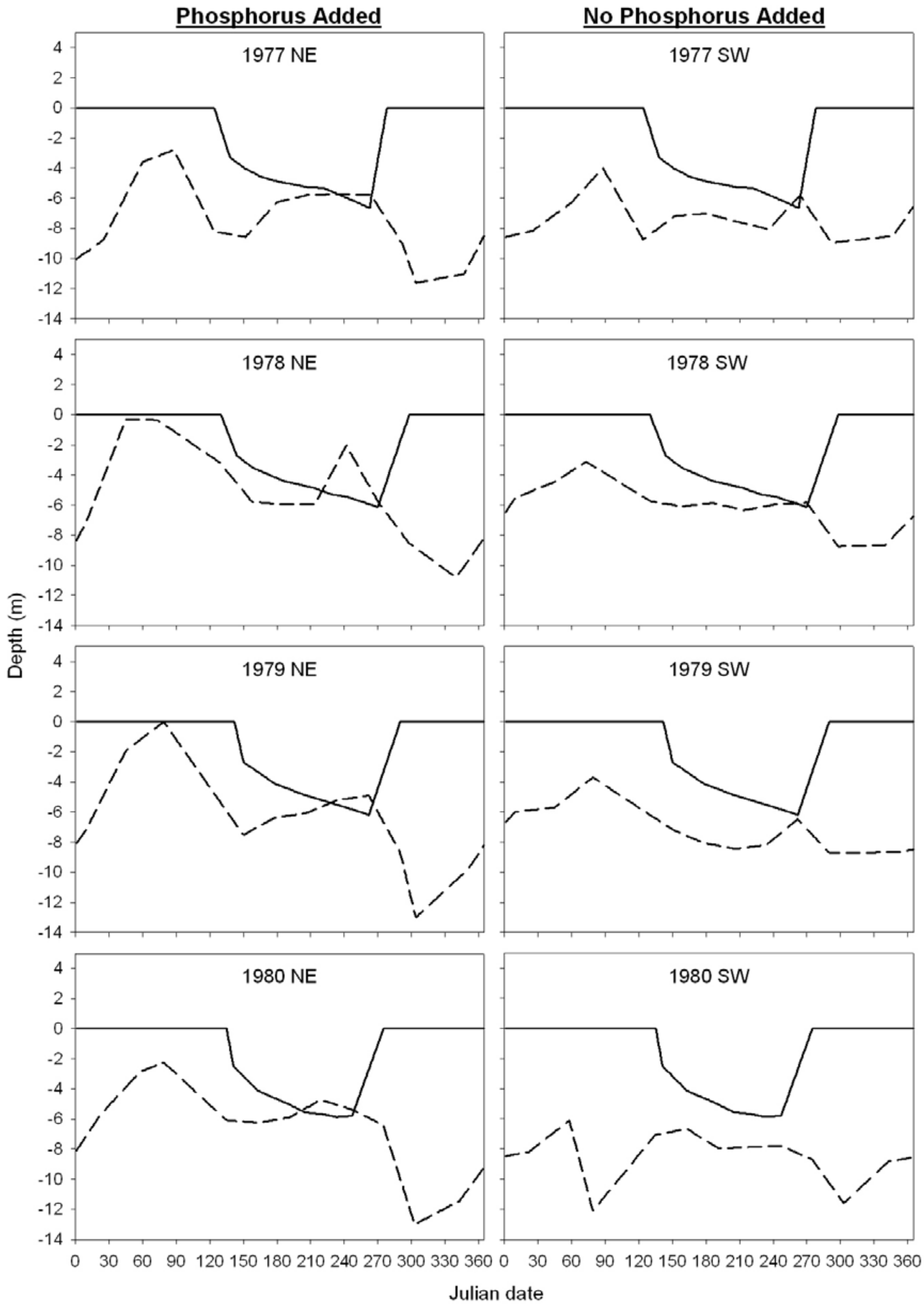

Figure 10. The daily interpolated depth where the temperature is ≤12 °C (solid line) and dissolved oxygen concentration of 4 mg/L (dashed line) in the northeast basin (NE) and the southwest basin (SW) during the eutrophication experiment.

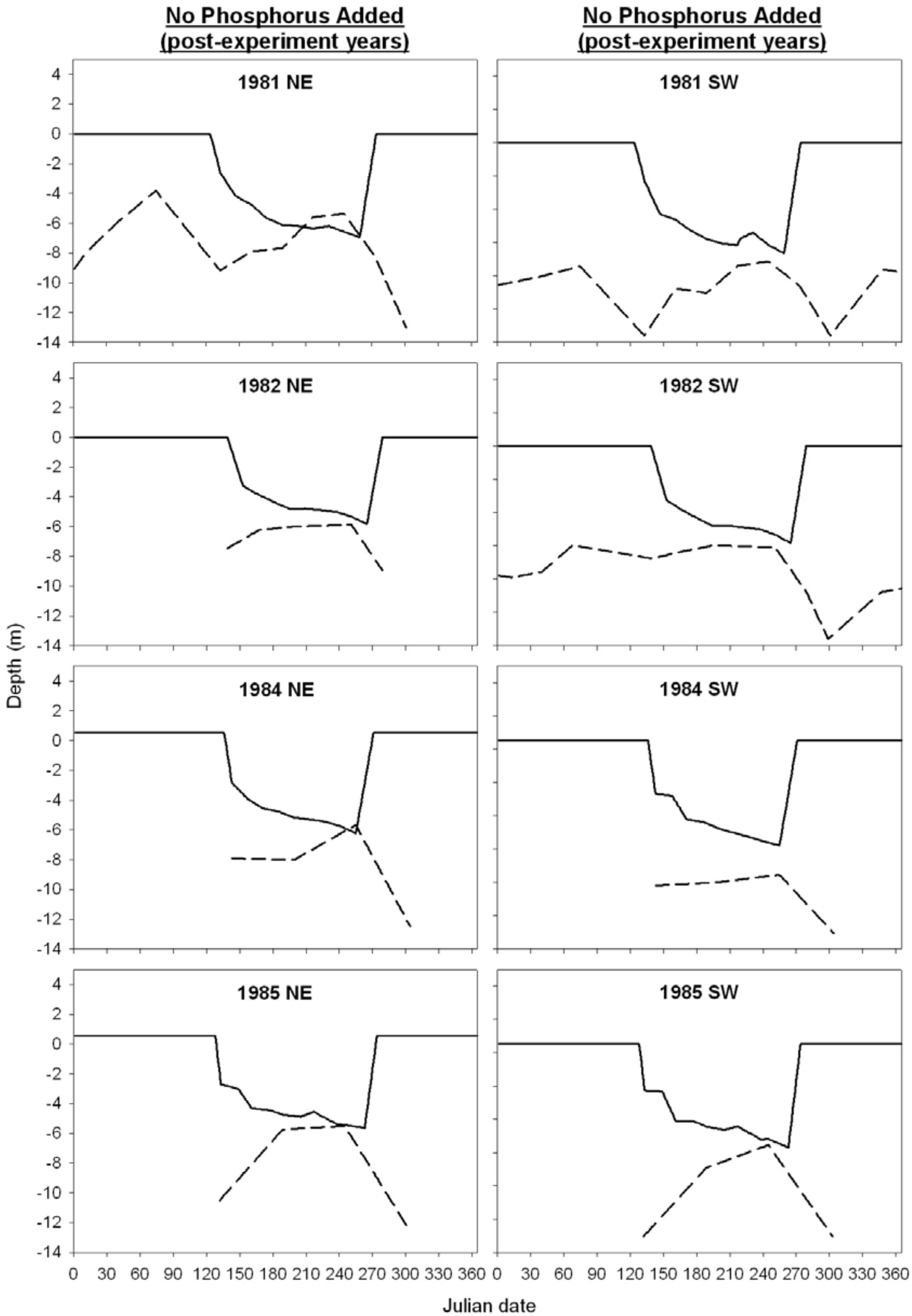

Figure 11. The daily interpolated depth where the temperature is ≤12 °C (solid line) and dissolved oxygen concentration of 4 mg/L (dashed line) in the northeast basin (NE) and the southwest basin (SW) during the post-eutrophication years.

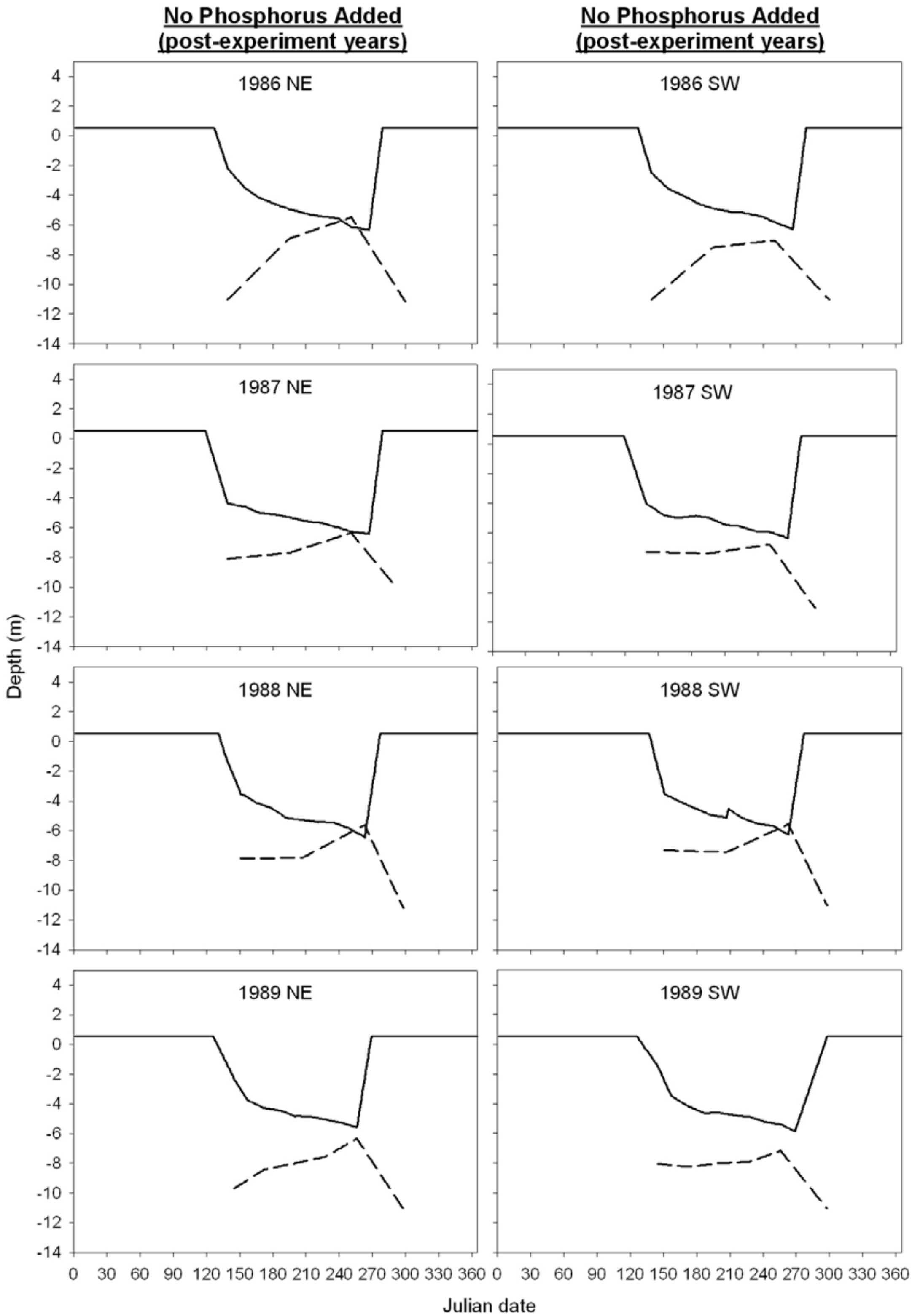

Figure 12. The daily interpolated depth where the temperature is ≤12 °C (solid line) and dissolved oxygen concentration of 4 mg/L (dashed line) in the northeast basin (NE) and the southwest basin (SW) during the post-eutrophication years.

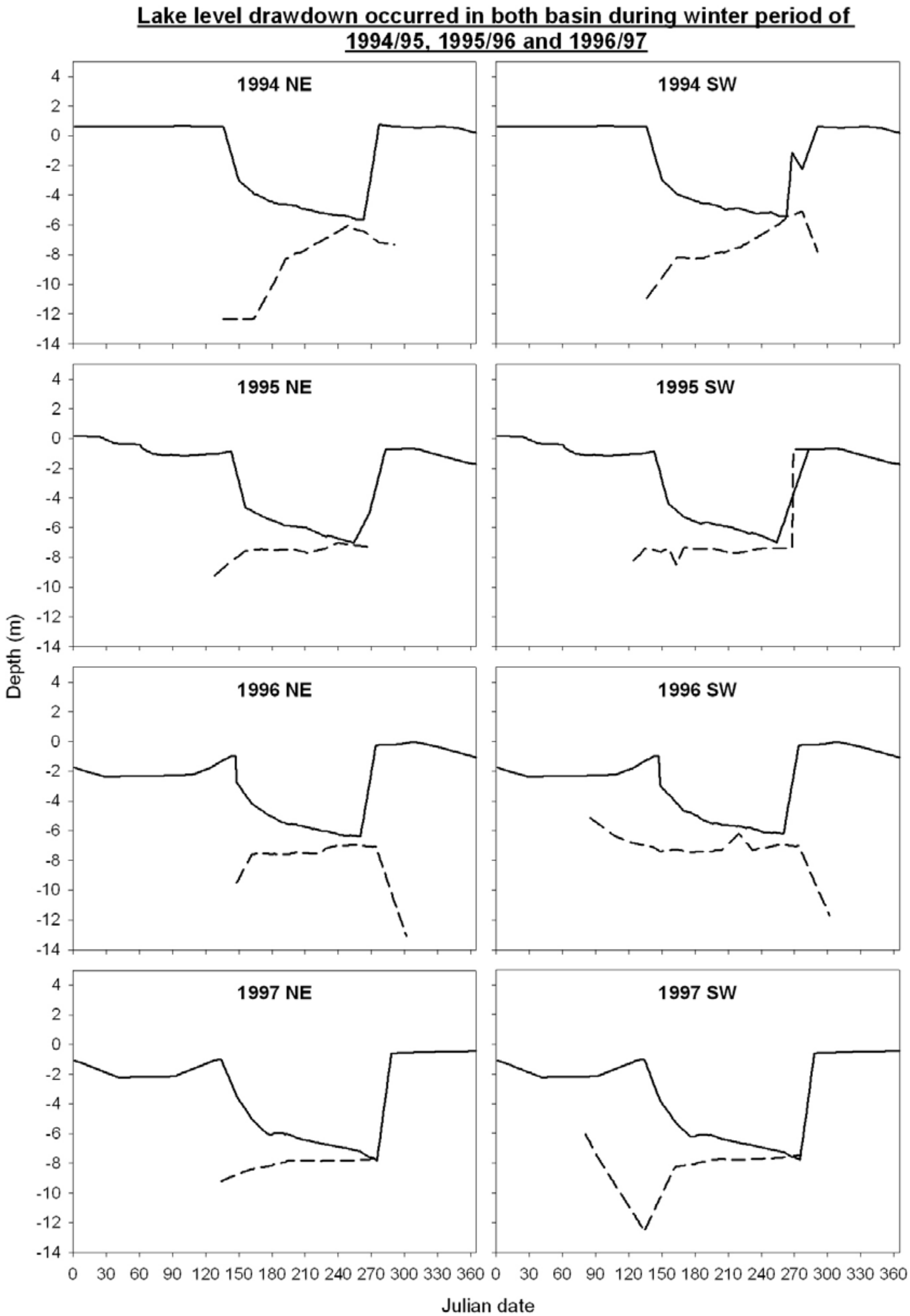

Figure 13. The daily interpolated depth where the temperature is ≤12 °C (solid line) and dissolved oxygen concentration of 4 mg/L (dashed line) in the northeast basin (NE) and the southwest basin (SW) during the lake water level drawdown experiment.

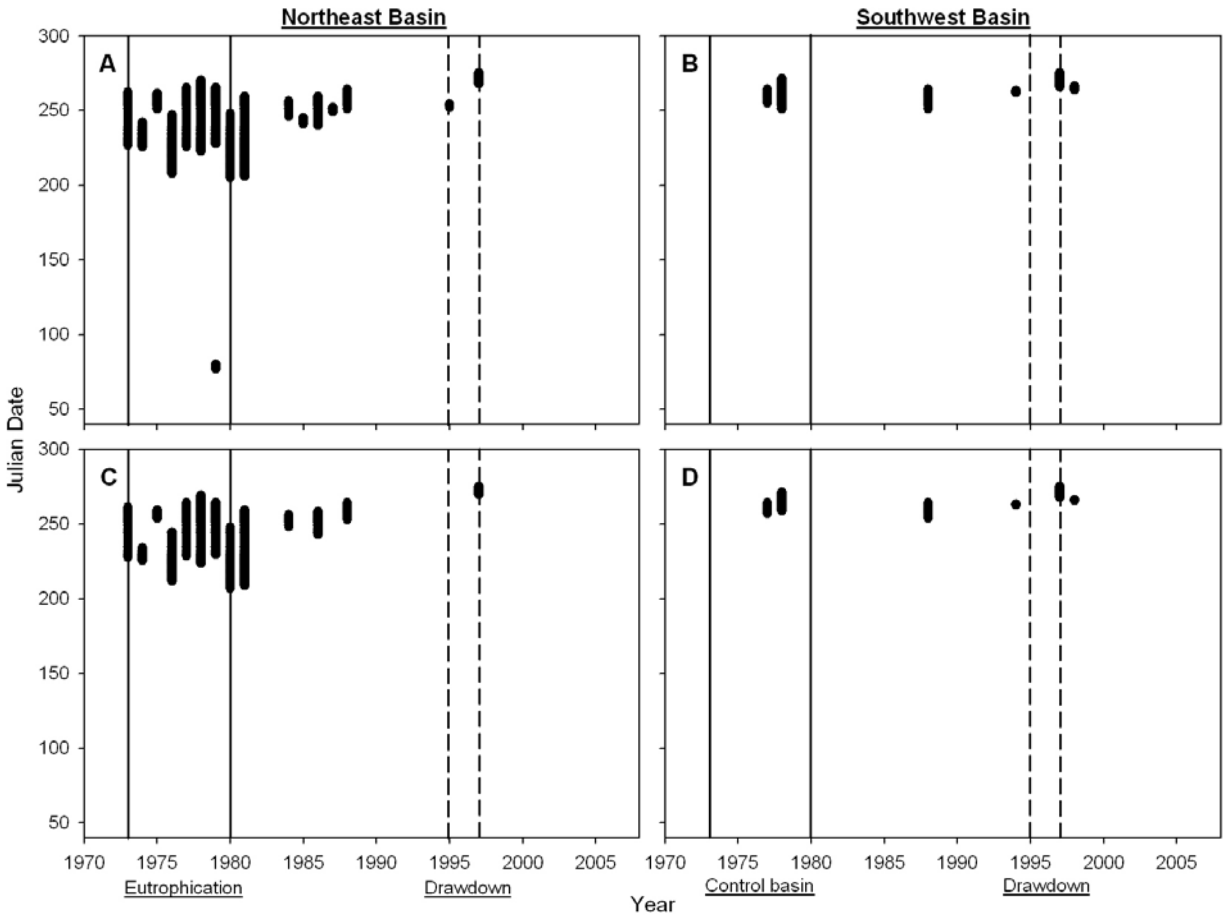

Figure 14. The seasonal timing and number of days that the optimal foraging habitat was less than 1% of the total lake area in the northeast basin (A) and southwest basin (B) as well as the timing and number of days the optimal physiological habitat was less than 1% of the total lake volume in the northeast (C) and southwest basin (D). Years within the vertical solid and dashed lines represent the years of the eutrophication and water level drawdown experiments, respectively.

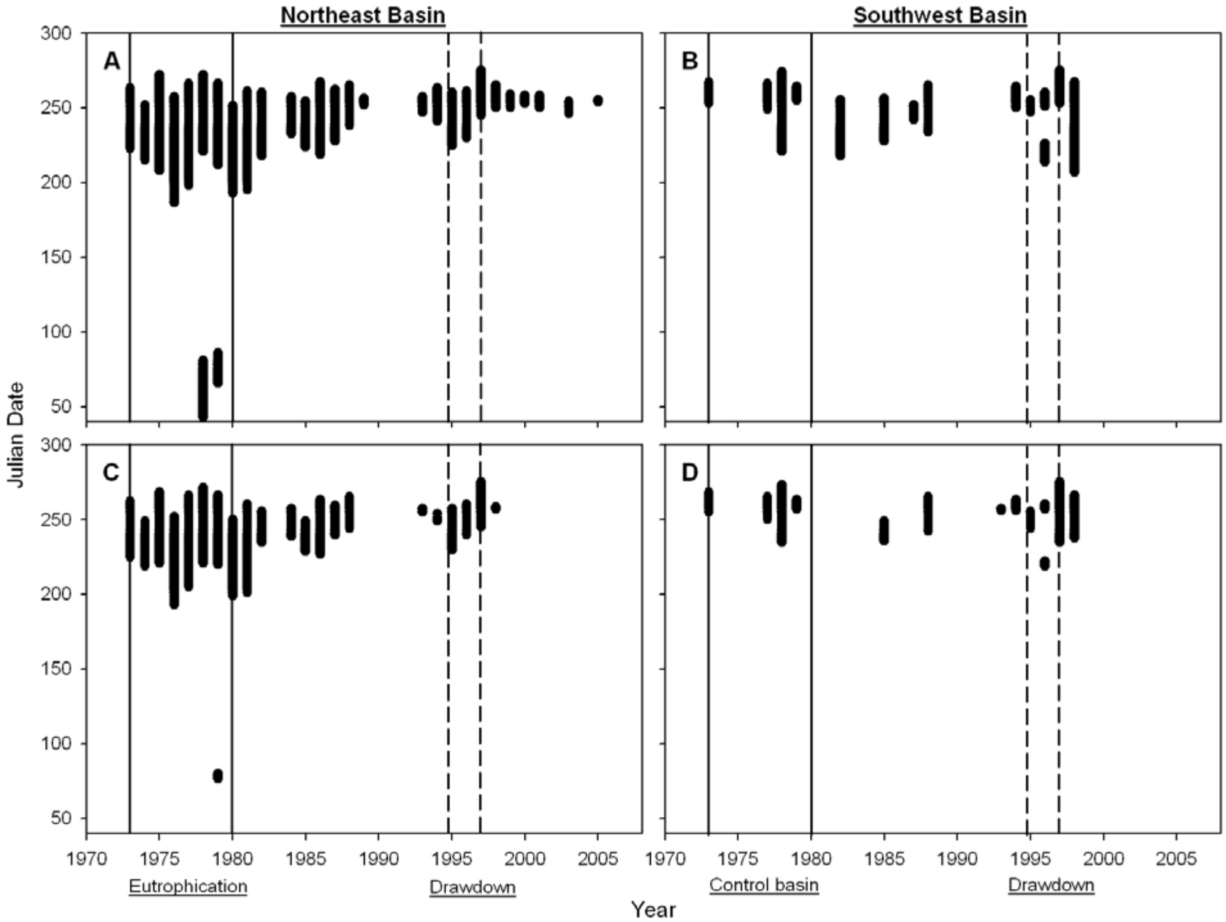

Figure 15. The seasonal timing and number of days that the optimal foraging habitat was less than 5% of the total lake area in the northeast basin (A) and southwest basin (B) as well as the timing and number of days the optimal physiological habitat was less than 5% of the total lake volume in the northeast (C) and southwest basin (D). Years within the vertical solid and dashed lines represent the years of the eutrophication and water level drawdown experiments, respectively.

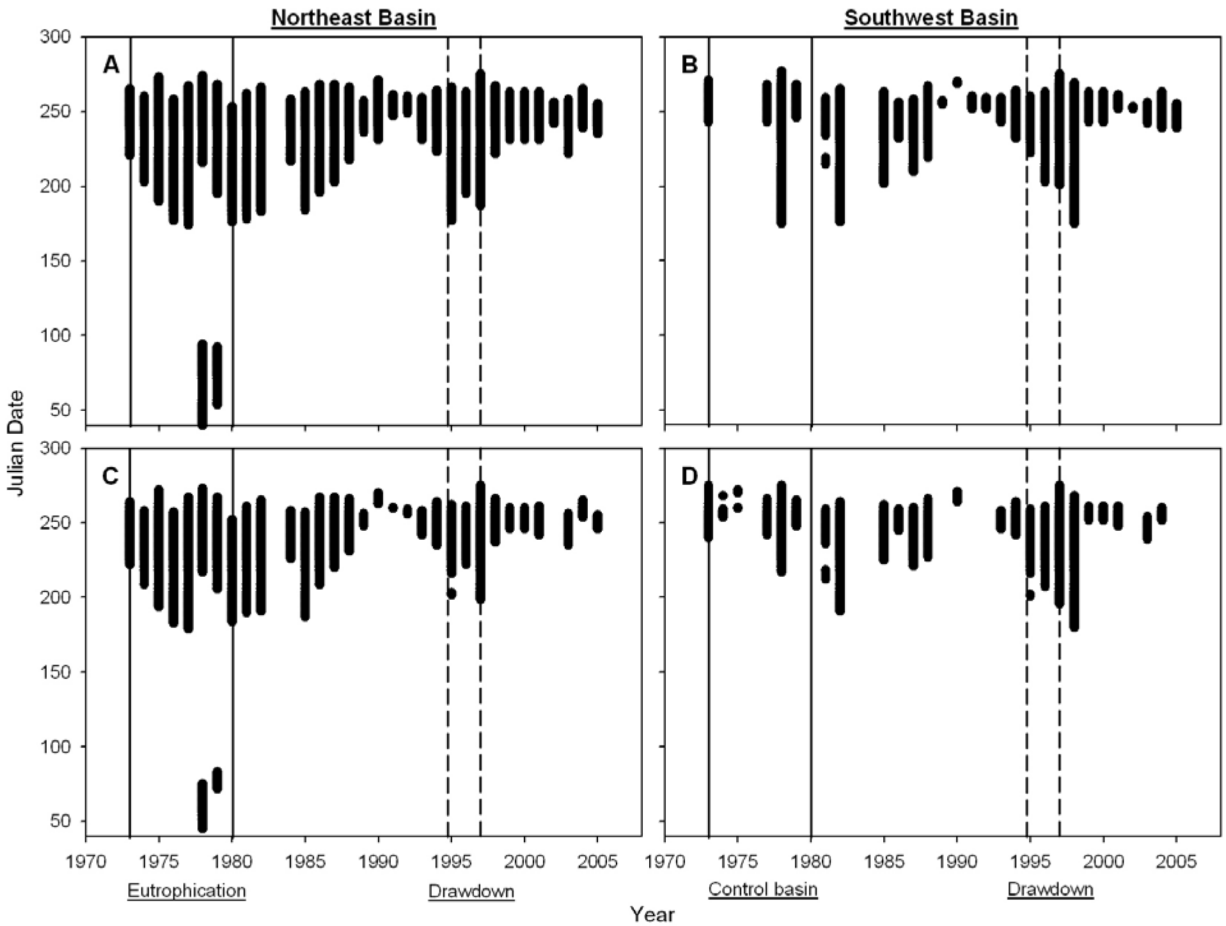

Figure 16. The seasonal timing and number of days that the optimal foraging habitat was less than 10% of the total lake area in the northeast basin (A) and southwest basin (B) as well as the timing and number of days the optimal physiological habitat was less than 10% of the total lake volume in the northeast (C) and southwest basin (D). Years within the vertical solid and dashed lines represent the years of the eutrophication and water level drawdown experiments, respectively.

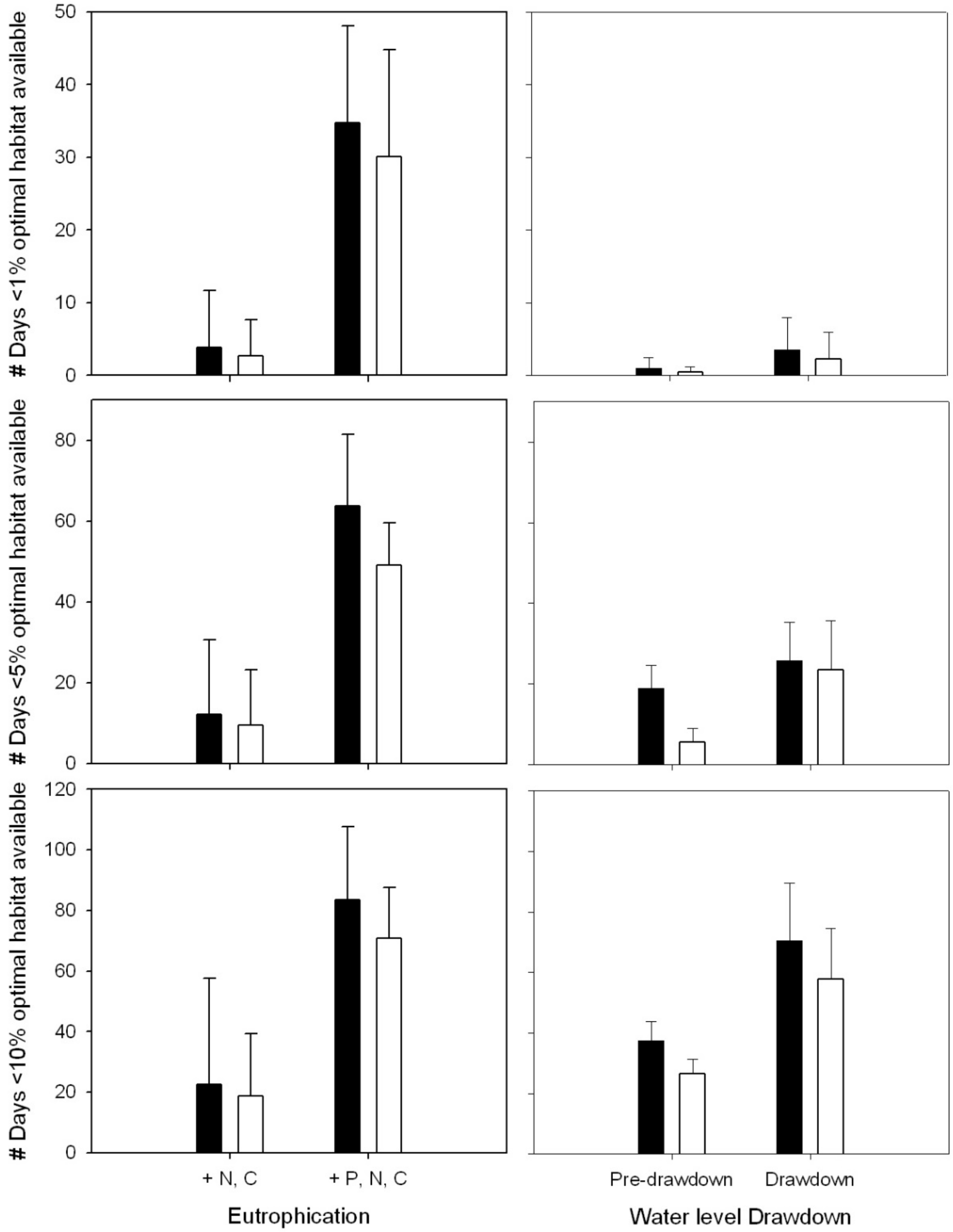

Figure 17. Number of days (±SD) that optimal foraging (black) and physiological (white) habitats were less than 1, 5 and 10% in the southwest basin (+N, C) and northeast basin (+P, N,C) during the eutrophication experiment (1973 to 1980) and in years prior to the drawdown experiment (1989, 1990 and 1994) and during the water level drawdown experiment (1995 to 1997). The letters N, C, and P indicate whether the basin received nitrogen, carbon, or phosphorus additions, respectively.

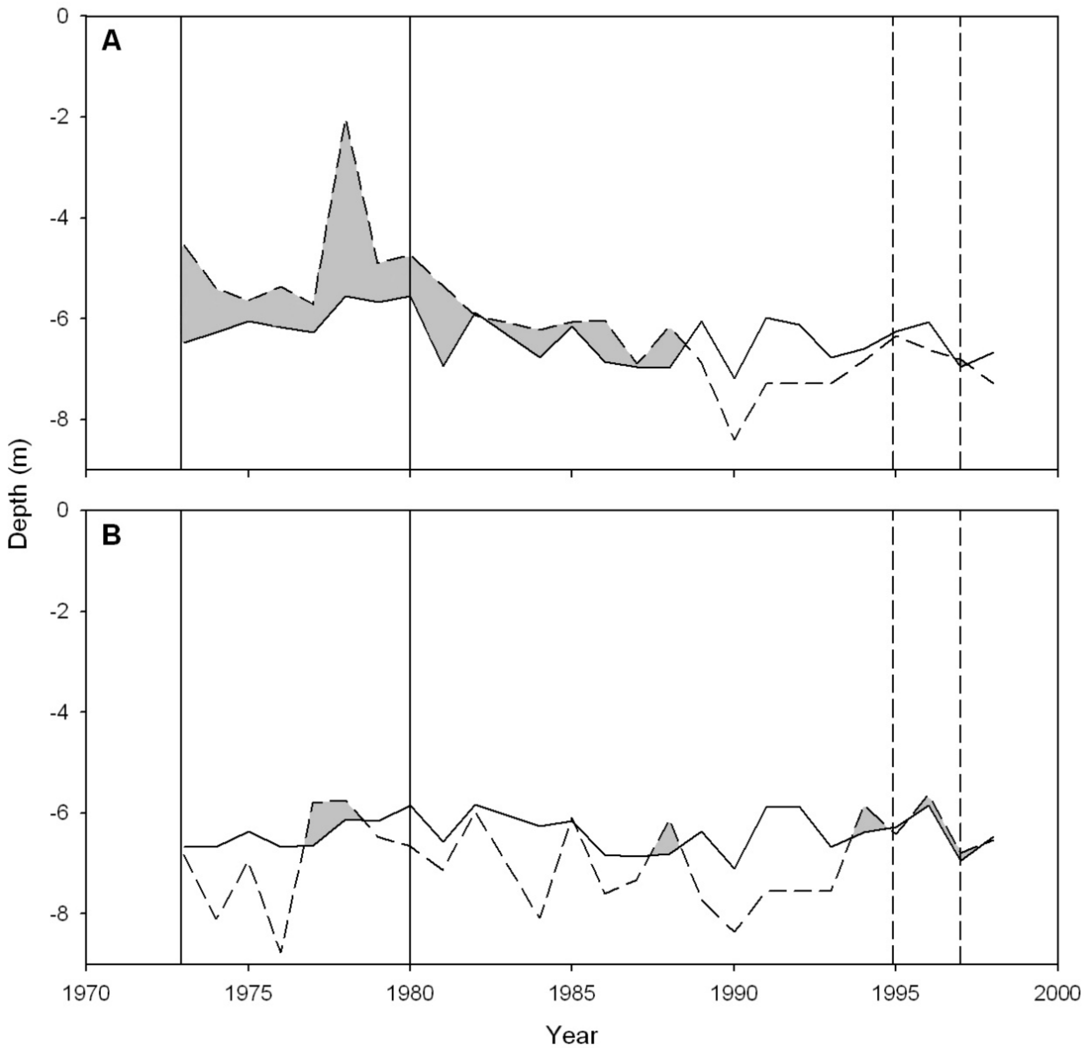

Figure 18. Annual maximum depth of 12 °C (solid line) and minimum depth of 4 mg/L dissolved oxygen (dashed line) from 1973 to 1998 in the northeast basin (A) and southwest basin (B). Years within the vertical solid and dashed lines represent the years of the eutrophication and water level drawdown experiments, respectively. Shaded portions indicate where, for at least a portion of the year, no optimal Lake Whitefish habitat was present within the lake. Solid vertical bars indicate the time of the eutrophication experiment, while dashed vertical bars represent the timing of the lake drawdown experiment.

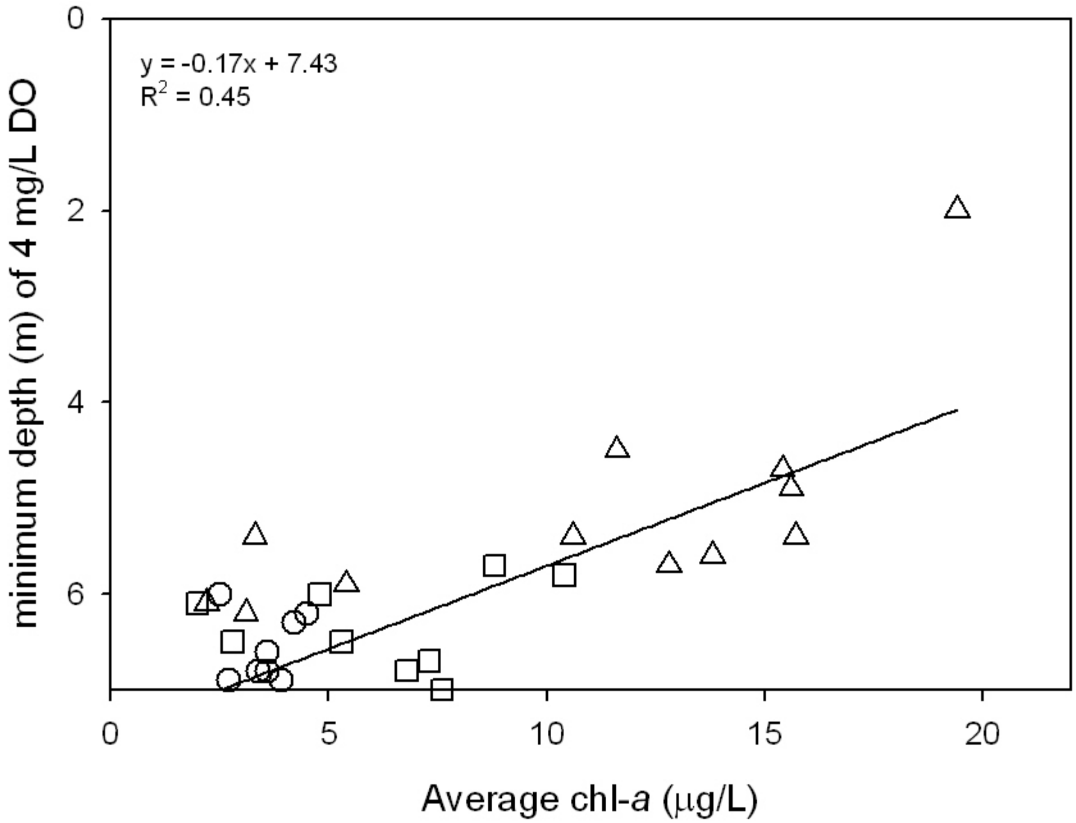

Figure 19. Correlation between the average chlorophyll-*a* (chl-*a*) concentrations and the minimum depth of 4 mg/L dissolved oxygen (DO) collected in the northeast basin (Δ), the southwest basin (□) and with the curtain removed (○) within the Julian date 121-304 timeframe throughout the sampling years 1973 to 1997.

References

Beamish, R.J. 1972. Design of a trapnet for sampling shallow water habitats. Fisheries Research Board of Canada Technical Reports **305**: 14p.

Bégout Anras, M.L., Cooley, P.M., Bodaly, R.A., Anras, L., and Fudge, R.J.P. 1999. Movement and habitat use by lake whitefish during spawning in a Boreal Lake: Integrating acoustic telemetry and geographic information systems. Transactions of the American Fisheries Society **128**(5): 939-952.

Bernatchez, L., and Dodson, J.J. 1985. Influence of temperature and current speed on the swimming capacity of Lake Whitefish (*Coregonus clupeaformis*) and Cisco (*C. artedii*). Canadian Journal of Fisheries and Aquatic Sciences **42**: 1522-1529.

Blanchfield, P.J., Paterson, M.J., Shearer, J.A., and Schindler, D.W. 2009. Johnson and Vallentyne's legacy: 40 years of aquatic research at the Experimental Lakes Area. Canadian Journal of Fisheries and Aquatic Sciences **66**: 1831-1836.

Carl, L.M., and McGuiness, F. 2006. Lake whitefish and lake herrinf population structure and niche in ten south-central Ontario lakes. Environmental Biology of Fishes **75**(3): 315-323.

Christie, G.G., and Regier, H.A. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Canadian Journal of Fisheries and Aquatic Sciences **45**: 301-314.

Cleugh, T.R., and Hauser, B.W. 1971. Results of the initial survey of the Experimental Lakes Area, northwestern Ontario. Journal of the Fisheries Research Board of Canada **28**: 123-128.

Cooper, G.P., and Fuller, J.L. 1945. A biological survey of Moosehead Lake and Haymock Lake, Maine, Maine Department of Inland Fisheries and Game.

Davies, I.J. 1980. Relationships between dipteran emergence and phytoplankton production in the Experimental Lakes Area, northwestern Ontario. Canadian Journal of Fisheries and Aquatic Sciences **37**: 523-533.

Davison, R.C., Breese, W.P., Warren, C.E., and Doudoroff, P. 1959. Experiments on the dissolved oxygen requirements of coldwater fishes. Sewage and Industrial Wastes **31**: 950-966.

Dell, M.B. 1968. A new fish tag and rapid cartridge fed applicator. Transactions of the American Fisheries Society **97**: 57-59.

Dillon, P.J., Clark, B.J., Molot, L.A., and Evans, H.E. 2003. Predicting the location of optimal habitat boundaries of lake trout (*Salvelinus namaycush*) in Canadian shield lakes. Canadian Journal of Fisheries and Aquatic Sciences **60**(8): 959-970.

Downing, J.A., Plante, C., and Lalonde, S. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Canadian Journal of Fisheries and Aquatic Sciences **47**: 1929-1936.

Dubois, J., and Dziedzic, A. 1989. Underwater sound detection applied to aquatic ethology: some results on coregonids and charr spawning sites in two subalpine lakes. Revue des Sciences de l'Eau **2**: 847-858.

Dumont, P., and Fortin, R. 1978. Some aspects of biology of great whitefish *Coregonus clupeaformis* in Lake Helene and Lake Nathalie, James Bay Territory. Canadian Journal of Zoology **56**: 1402-1411.

Edsall, T.A. 1999a. Preferred temperatures of juvenile lake whitefish. Journal of Great Lakes Research **25**(3): 583-588.

Edsall, T.A. 1999b. The growth-temperature relation of juvenile lake whitefish. Transactions of the American Fisheries Society **128**(5): 962-964.

Evans, D.O., Casselman, J.M., and Wilcox, C.C. 1991. Effects of exploitation, loss of nursery habitat, and stocking on the dynamics and productivity of lake trout in Ontario lakes., Ontario Ministry of Natural Resources, Toronto, ON.

Ferguson, R.G. 1958. The preferred temperature of fish and their mi-summer distribution in temperate lakes and streams. Journal of the Fisheries Research Board of Canada **15**(607-624).

Findlay, D.L., and Kasian, S.E.M. 1987. Phytoplankton community responses to nutrient addition in Lake 226, Experimental Lakes Area, northwestern Ontario. Canadian Journal of Fisheries and Aquatic Sciences **44**(Suppl. 1): 35-46.

Fry, F.E.J. 1947. Effects of the environment on animal activity, University of Toronto, Biological Series 55, Publication of the Ontario Fisheries Research Laboratory 68.

Fudge, R.J.P., and Bodaly, R.A. 1984. Postimpoundment winter sedimentation and survival of lake whitefish (Coregonus clupeaformis) eggs in Southern Indian Lake, Manitoba. Canadian Journal of Fisheries and Aquatic Sciences **41**: 701-705.

Hart, J.L. 1930. The spawning and early life history of the whitefish, *Coregonus clupeaformis* (Mitchill), in the Bat of Quinte, Ontario. Contributions in Canadian Biology and Fisheries **6**: 165-214.

Hoagman, W.W. 1974. Vital activity parameters are related to the early life history of larval and post larval whitefish (*Coregonus clupeaformis*). *In* The early life history of fosh. *Edited by* J.H.S. Baxter. Springer Verlag, New York, NY.

Jobling, M. 1981. Temperature tolerance and the final preferendum - rapid methods of assessment of optimum growth temperatures. Journal of Fish Biology **19**: 439-455.

Madenjian, C.P., O'Connor, D.V., Pothoven, S.A., Schneeberger, P.J., Rediske, R.R., O'Keefe, J.P., Bergstedt, R.A., Argyle, R.L., and Brandt, S.B. 2006. Evaluation of a lake whitefish bioenergetics model. Transactions of the American Fisheries Society **135**(1): 61-75.

Mills, K.H. 1985. Responses of lake whitefish (*Coregonus cleupeaformis*) to fertilization of Lake 226, the Experimental Lakes Area. Canadian Journal of Fisheries and Aquatic Sciences **42**: 129-138.

Mills, K.H., and Chalanchuk, S.M. 1987. Population dynamics of lake whitefish (*Coregonus clupeaformis*) during and after the fertilization of Lake 226, the Experimental Lakes Area. Canadian Journal of Fisheries and Aquatic Sciences **44**: 55-63.

Mills, K.H., Chalanchuk, S.M., Allan, D.J., and Bodaly, R.A. 2002a. Abundance, survival, condition, and recruitment of lake whitefish (*Coregonus clupeaformis*) in a lake subjected to winter drawdown. Archives of hydrobiology special issues - advances in limnology **57**: 209-219.

Mills, K.H., Chalanchuk, S.M., Findlay, D.L., Allan, D.J., and McColloch, B.R. 2002b. Condition, recruitment, and abundance of lake whitefish (*Coregonus clupeaformis*) in a fertilized lake. Archives of hydrobiology special issues - advances in limnology **57**: 423-433.

Molot, L.A., Dillon, P.J., Clark, B.J., and Neary, B.P. 1992. Predicting end-of-summer oxygen profiles in stratified lakes. Canadian Journal of Fisheries and Aquatic Sciences **49**: 2363-2372.

Nester, R.T., and Poe, T.P. 1984. Predation on lake whitefish eggs by longnose suckers. Journal of Great Lakes Research **10**: 327-328.

Paterson, M.J., Findlay, D.L., Beaty, K., Findlay, W., Schindler, E.U., Stainton, M., and McCullough, G. 1997. Changes in the planktonic food web of a new experimental reservoir. Canadian Journal of Fisheries and Aquatic Sciences **54**: 1088-1102.

Plumb, J.M., and Blanchfield, P.J. 2009. Performance of temperature and dissolved oxygen criteria to predict habitat use by lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences **66**: 2011-2023.

Rennie, M.D., Johnson, T.B., and Sprules, W.G. 2012. Energy acquisition and allocation patterns of lake whitefish (*Coregonus clupeaformis*) are modified when dreissenids are present. Canadian Journal of Fisheries and Aquatic Sciences **69**: 41-59.

Rosenberg, D.M., Bodaly, R.A., Hecky, R.E., and Newbury, R.W. 1987. The environmental assessment of hydroelectric impoundments and diversions in Canada. Canadian Bulletin of Fisheries and Aquatic Sciences **215**: 71-104.

Schearer, J.A., Fee, E.J., DeBruyn, E.R., and DeClercq, D.R. 1987. Phytoplankton productivity changes in a small, double-basin lake in response to termination of experimental fertilization. Canadian Journal of Fisheries and Aquatic Sciences **44**(Suppl. 1): 55-63.

Schindler, D.W. 1974. Eutrophication and recovery in the Experimental Lakes: implications for lake management. Science **184**: 897-899.

Schindler, D.W., and Fee, E.J. 1974. Experimental Lakes Area: whole lakes experiments in eutrophication. Journal of the Fisheries Research Board of Canada 31: 937-953.

Tompkins, F.T., and Fraser, J.M. 1950. The preferred temperature of a sample of Great Lakes whitefish (Coregonus clupeaformis). Department of Zoology, University of Toronto, Toronto, ON.

Turner, M.A., Huebert, D.B., Findlay, D.L., Hendezel, L.L., Jansen, W.A., Bodaly, R.A., Armstrong, L.M., and Kasian, S.E.M. 2005. Divergent impacts of experimental lake-level drawdown on planktonic and benthic plant communities in a boreal forest lake. Canadian Journal of Fisheries and Aquatic Sciences 62: 991-1003.

White, W.J., and Beamish, R.J. 1972. A simple fish tag suitable for long-term marking experiments. Journal of the Fisheries Research Board of Canada 29: 339-341.